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THE GENITALIC, ALLOZYMIC, AND CONCHOLOGICAL EVOLUTION OF THE EASTERN NORTH AMERICAN TRIODOPSINAE (GASTROPODA: PULMONATA: POLYGYRIDAE)

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ABSTRACT

The 40 species of triodopsines in eastern North America are useful for evolutionary studies because of their diverse genitalic and conchological radiations. Previous monographs were based on shells, many features of which are subject to convergence.

Dissection of the uneverted penial tubes revealed a morphological diversity that was classified into 10 characters comprising 60 character states. Cladistic analysis yielded a single most parsimonious tree with a consistency index of .970.

Starch-gel electrophoresis of foot tissue detected 74 alleles among 16 loci. Cladistic analysis using the independent alleles model resulted in a consensus, maximum-parsimony tree with a consistency index of .950. Electrophoresed populations were divided into two equal subsets for rooted distance-Wagner analyses based on Prevosti distances. The resulting trees had cophenetic correlations of .897 and .883.

The anatomical and allelic cladograms and the two genetic-distance trees were weighted according to the sizes and reliabilities of the data bases used in their construction. Branch-by-branch comparison of the four weighted trees produced a consensus phylogeny that was quite robust, and with only a few species remaining problematic due to incomplete or conflicting data.

Supraspecific revision based on this consensus phylogeny divides eastern triodopsines into four genera: *Neohelix* von Ihering, 1892; *Triodopsis* Rafinesque, 1819; *Webbhelix* Emberton, new genus; and *Xolotrema* (Rafinesque, 1819). The revision differs most strongly from previous classifications in its species groupings within the large genus *Triodopsis*.

Revision of the *Neohelix albolabris* group (the "white-lipped land snail"), based on 46 populations, discovered two new taxa: *N. solemi* and *N. albolabris bogani*. A cladogram (consistency index 1.00) based on genitalic morphometrics formed the basis for revision, which split the group into the *albolabris* and *alleni* groups. Shell differences among taxa are subtle and occasionally unreliable for identification, according to a multivariate discriminant analysis.

Genitalic and geographic comparisons between 25 pairs of sister taxa detected a pattern: sister taxa with virtually identical penial morphologies generally have peripatric geographic ranges, those slightly different are generally allopatric, those moderately different are sympatric, whereas those greatly different are parapatric. Population-level comparisons for 12 species failed to find any trace of reproductive character displacement. These results, as well as the pattern of genitalic convergences and the geographic stability of within-species genitalic morphology, led to the hypotheses that (1) peripheral isolates generally do not differentiate, (2) vicariant isolates generally differentiate slowly, (3) differentiation due to reproductive character displacement is moderate at most, and (4) major differentiation is rare, rapid, and occurs in isolates.

Shell evolution's pattern and inferred process differs among taxonomic levels. Genera show general conchological stasis despite extensive, overlapping ecological radiations; the process is probably canalization. Species groups show mosaic distributions of minor shell characters; the process is presumably genetic indeterminism of canalized developmental programs. Species and populations show two patterns: patchy, non-clinal variation in size and some aspects of shape and sculpture, probably induced by local microclimates; and iterated environmental correlations—e.g., between apertural obstruction and ground moisture, spire flatness and crevice-dwelling, and periostracal glossiness and water—presumably due to natural selection.

The nature and definition of a species in eastern triodopsines remains both a problem and a fruitful avenue of research. The many sympatric shell convergences between eastern triodopsines and the polygyrine genus *Mesodon* provide naturally replicated experiments in evolutionary morphology.

Key words: snails; evolution; genitalia; allozymes; shells; cladistics; character displacement; natural selection; convergence.

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INTRODUCTION

The Polygyridae are an autochthonous North American family of pulmonate land snails comprising approximately 260 species currently classified into 14 genera in 3 subfamilies (Pilsbry, 1940; Webb, 1954a; Hubricht, 1985; Richardson, 1986). This paper deals with eastern members of the subfamily Triodopsinae. Western triodopsines comprise the single genus *Vespericola* Pilsbry, 1939, which has some 9 species and ranges along the Pacific coastal zone from southern Alaska to northern California (Pilsbry, 1940; Roth, 1984) Eastern triodopsines, as revised in this paper, comprise the four genera *Neohelix* von Ihering, 1892, (7 species); *Triodopsis* Rafinesque, 1819 (26 species, not including the Siberian *"Triodopsis" supersonatum*—see Emberton, 1986); *Webbhelix* Emberton, new genus (1 species); and *Xolotrema* Rafinesque, 1819 (5 species). They range throughout temperate North America east of the Great Plains.

The eastern triodopsines are a common, large (8–40 mm), and sometimes dominant element of the leaf-litter invertebrate fauna. Eastern triodopsines are important for several reasons. (1) Because of their multiple sympatric conchological convergences on the polygyrine genus *Mesodon* (Pilsbry, 1940; Solem, 1976; Emberton, 1986), they contain superb naturally replicated experiments in evolutionary morphology (see Emberton, 1986). (2) Their diversity of complex penial morphologies (Webb, 1947–1980) makes them useful for testing the recent general hypotheses of Eberhardt (1985) concerning genitalic evolution. (3) Their substantial conchological variation (e.g., Vagvolgyi, 1968) makes them useful for advancing our very limited knowledge of the adaptive vs. ecologically induced components of shell shape in land snails (see review by Goodfriend, 1986). (4) The large size, high density, low vagility, and easy markability of many species make them useful subjects for generalizable studies in population biology (McCracken, 1976), population genetics (McCracken, 1980; McCracken & Brussard, 1980), life history and ecology (Vail, 1978; Emberton, 1981), and anatomy (Simpson, 1901; Emberton, 1985). (5) They are economically and ecologically important as the intermediate hosts of sometimes lethal parasites of elk, deer, and other

game and non-game mammals (e.g., Maze & Johnstone, 1986). (6) Their larger species are potentially of economic value as sources of anti-A agglutinin for typing human blood (Miles, 1983).

Previous monographic treatments of the eastern American triodopsines (Pilsbry, 1940; Vagvolgyi, 1968) were conchological.

The purposes of this paper are (1) to derive a robust phylogenetic hypothesis for the eastern triodopsines using two independent data sets: male genitalia and allozymes; (2) to revise the eastern triodopsines above the species level, based on this phylogeny; (3) to analyze phylogenetic patterns of variation in both genitalia and shell morphology and to generate hypotheses about the evolutionary processes which produced these patterns; and (4) to further revise the *Neohelix albolabris* group to the subspecies level.

The *Neohelix albolabris* group contains the largest, most conspicuous triodopsine snails. McCracken & Brussard's (1980) electrophoretic survey of "the white-lipped snail" (*Neohelix albolabris* [Say, 1816]) showed a confusing geographic diversity in this group which pointed out the need for taxonomic resolution using anatomical and conchological characters.

Penial morphology, presumed to be important in species recognition and of great potential value for the systematics of eastern triodopsines (Pilsbry, 1940; Webb, 1947–1980; Solem, 1976), has previously been exploited only to a very limited extent. There are three ways of studying penial sculpture in land pulmonates (Fig. 1): by killing and fixing the snail relaxed and extended from its shell, then dissecting open the uneverted penial tube (the dissective method); by killing and fixing the snail *in copulo* so as to keep its penis fully everted (the evertive method); or by clearing, staining, and mounting the uneverted penial tube (the slide-mount nethod). Until the beginning of Webb's publications in 1947, the only triodopsine species for which details of penial sculpture were known was *Neohelix albolabris,* illustrated by Binney (1851), Pilsbry (1894, 1940), and Simpson (1901); in all four of these papers it was studied by the dissective method. Webb (1947, 1948, 1952, 1954, 1959) studied 12 species and Grimm (1975) studied one species of eastern triodopsines by the evertive method and illustrated the general aspects of penial sculpture. Solem (1976) illustrated the dissected uneverted penial tubes of three species, thereby redemonstrating the efficacy of the dissective method and showing the wealth of sculptural detail omitted by Webb and Grimm.

The dissective method is in many respects superior to both the evertive and slide-mount methods (Fig. 1). Waiting for penial eversion, then killing and fixing without distorting the soft tissues, is labor-intensive and yields little additional information (but see Character 10 below). Clearing and mounting the uneverted penial tube is more time-consuming than cutting it open, and is much less effective for interpreting complex sculpture because of three-dimensional overlap further distorted by viewing through other tissues.

Thus the most obvious source of useful characters for phylogenetic analysis was penial sculpture as viewed by the dissective method. For this character set, 27 of the 40 species of eastern triodopsines had never been examined before, and, of those that had, only 3 had been illustrated in sufficient detail.

The other character set chosen for phylogenetic analysis was that of allozymes as viewed by horizontal starch-gel electrophoresis. Regardless of whether allozymes are adaptively significant (e.g., Hochachka & Somero, 1984; Nevo & Bar, 1976; Nevo et al., 1981; Nevo et al., 1982) or adaptively neutral (e.g., Kimura, 1979, 1982), they offer a morphological data set virtually independent of penial morphology. Four species of eastern triodopsines had previously been electrophoresed (McCracken & Brussard, 1980, as reevaluated by Emberton, McCracken & Wooden, in preparation). These were examined at 8 variable loci that showed sufficient variation to bode success for applying electrophoresis to the systematics of the entire group. Certain alleles of some loci had also been shown to be genetically heritable (McCracken, 1976, 1980).

The value of allozymes for systematic studies is well established (e.g., Avise, 1975; Sarich, 1977; Throckmorton, 1978; Davis, 1978; Nei et al., 1983; Patton & Avise, 1983; Buth, 1984). Although land-snail allozymes have been used extensively for studies on population genetics and breeding systems (reviewed by Clarke, 1978; Selander & Ochman, 1983; Selander & Whittam, 1983), only twice before have they been used for extensive phylogenetic studies. In neither of these previous efforts—on West Indian *Cerion* by Gould et al. (1975), and on Moorean *Partula*

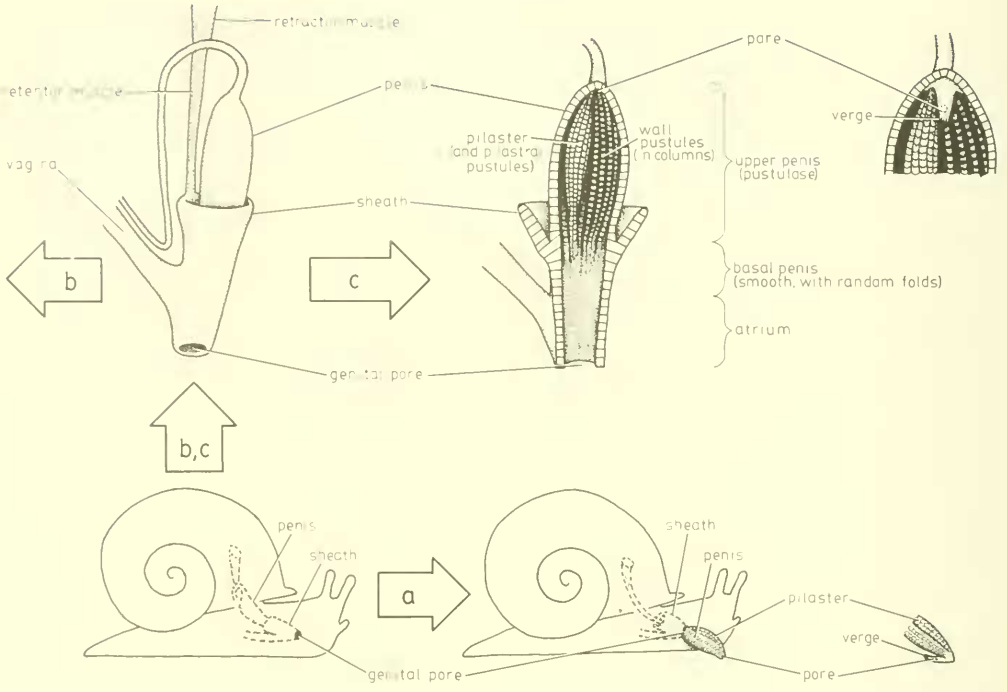

FIG. 1. Penial morphology of east American triodopsines: its major features and the three alternative methods for studying the sculpture of its functional surface. **a.** The evertive method. **b.** The slide-mount method (clearing and staining). **c.** The dissective method.

by Johnson et al. (1977)—was sufficient electrophoretic variation found to be of much value in reconstructing species-level phylogenies. Both these groups, however, appear to be relatively recent radiations (Woodruff & Gould, 1978; Murray & Clarke, 1980), much younger than eastern triodopsines (see Emberton, 1986).

Thus penial morphology and allozymes were chosen because of their independence from each other and because each promised to be rich in phylogenetically useful variation. To avoid circularity in evaluating conchological evolution, no shell characters were used for phylogenetic analysis.

Time constraints prohibited the use of other morphological character sets that previous studies had indicated were less information-rich than penial morphology and allozymes. Concerning radulae, Solem's (1976) study of three triodopsines (two of them sympatric) had found an "essential similarity", with, "in terms of basic structure and pattern of functioning, . . . no major differences between species, much less between genera". Likewise, Binney's (1878) sketches of the radulae of 9 other triodopsine species, although rather inadequate in detail, showed a similar lack of variation. The macro- and microstructure of the jaw promised little useful information, because Solem (1976) found "no significant differences" among three species of eastern triodopsines.

The size and shape of the hermaphroditic duct, talon, albumen gland, prostate, uterus, and spermatheca undergo such significant and extreme seasonal variation in one species of *Triodopsis* (Emberton, 1985) that the use of these characters for systematics would have had to have been cautious and labor-intensive. Likewise, considerable variations in the diameter and length of the ovotesticular lobes, the basal penis, the free oviduct, and the vagina correlate with changes in reproductive state (Emberton, 1985: figs. 5–7).

Preliminary studies (Emberton, unpublished data) showed that the internal structure of the functional vagina (the spermathecal or gametolytic duct) was identical in several triodopsine species. This lack of variation extended to several pairs of microsympatric species with similar shell sizes and penial morphology. The structure of the triodopsine functional vagina has been illustrated by

Binney (1851: pl. 7, fig. 4; pl. 8, fig. 3), Simpson (1901: pl. 8, fig. 11), and Grimm (1975: fig. 3A).

Technology for viewing the chromosomal bands of land snails (e.g., Babrakzai & Miller, 1975, 1984) seemed in too early a stage of development for a project of this scope. Simple chromosomal counts promised little insight, because an early study (Husted & Burch, 1947) of 17 species of polygyrids, including 6 triodopsines, found a diploid number of 58 in all except what was identified as *Triodopsis fraudulenta,* populations of which were reported to vary in diploid number from 58 to 62. Furthermore, the phylogenetic interpretation of chromosomal numbers can be highly problematic (e.g., Solem, 1978).

Thus this phylogenetic analysis of the eastern American triodopsines was restricted to male-genitalic and allozymic characters.

MATERIALS AND METHODS

Taxa studied

Neohelix von Ihering, 1892
- *albolabris* (Say, 1816)
- *alleni* (Sampson, 1883)
- *dentifera* (Binney, 1837)
- *divesta* (Gould, 1848)
- *lioderma* (Pilsbry, 1902)
- *major* (Binney, 1837)
- *solemi* Emberton, new species

Triodopsis Rafinesque, 1819
- *alabamensis* (Pilsbry, 1902)
- *anteridon* (Pilsbry, 1940)
- *burchi* Hubricht, 1950
- claibornensis Lutz, 1950
- *complanata* (Pilsbry, 1898)
- *cragini* Call, 1886
- *discoidea* (Pilsbry, 1904)
- *fallax* (Say, 1825)
- *fraudulenta* (Pilsbry, 1894)
- *fulciden* Hubricht, 1952
- *henriettae* (Mazÿck, 1877)
- *hopetonensis* (Shuttleworth, 1852)
- *juxtidens* (Pilsbry, 1894)
- *messana* Hubricht, 1952
- *neglecta* (Pilsbry, 1899)
- *obsoleta* (Pilsbry, 1894)
- *palustris* Hubricht, 1958
- *pendula* Hubricht, 1952
- *picea* Hubricht, 1958
- *platysayoides* (Brooks, 1933)
- *rugosa* Brooks & MacMillan, 1940
- *soelneri* (Henderson, 1907)
- *tennesseensis* (Walker & Pilsbry, 1902)
- *tridentata* (Say, 1816)
- *vannostrandi* (Bland, 1875)
- vulgata (Pilsbry, 1940)
- *vultuosa* (Gould, 1848)

Webbhelix Emberton, new genus
- multilineata (Say, 1821)

Xolotrema Rafinesque, 1819
- *caroliniensis* (Lea, 1834)
- *denotata* (Férussac, 1821)
- *fosteri* (F. C. Baker, 1932)
- *obstricta* (Say, 1821)
- *occidentalis* (Pilsbry & Ferriss, 1907)

Collections

Principal field work was conducted April-June 1982 in the eastern United States ("GS" series), and was supplemented by collections from southeastern Ohio in March-July 1979 ("Ohio" series), from the lower Ohio River Valley in April 1980 ("H" series), and from the southern Appalachian area in March-June 1983 ("SC" series). All collections were donated to the Field Museum of Natural History, Chicago. County-level localities, field numbers, and catalog numbers of dissected and electrophoresed material are listed under each species in the systematic reviews in Appendices B and C. Detailed locality data are available from the author on request or from the Field Museum catalog. Snails in each lot were individually marked on their shells: 1, 2, 3, etc. for snails from which tissue samples were taken; and A, B, C, etc. for snails that were not tissue-sampled. Appendices B and C record which individual snails from each lot were dissected, electrophoresed, and illustrated anatomically and/or conchologically.

Additional anatomical material (total 18 lots) was borrowed from the Field Museum (FMNH), the Academy of Natural Sciences of Philadelphia (ANSP), and the private collection of Mr. Leslie Hubricht.

For the *Neohelix albolabris* and *alleni* groups, 41 populations were collected or borrowed, and 5 additional populations were studied from published anatomical illustrations.

Dissections

The uneverted penial tubes of 252 snails from 108 populations comprising all 40 of Hubricht's (1985) species were dissected. Most populations were collected in the early

spring, but to make a crude check for significant seasonal variation which might bias interspecific comparisons, three *T. tridentata* from Strouds Run State Park, Ohio, were dissected, each at a different stage in the life cycle of this species: mating-ready neoadult (FMNH 209209, specimen C); post-mating neoadult (FMNH 209536, specimen C); and overwintered, mating-ready, old adult (FMNH 209209, specimen D) (see Emberton, 1985).

Whenever possible, at least three adults of each species were dissected. Because of the limitations of available material, however, 10 species were represented by only two dissections each *(X. obstricta, X. caroliniensis, T. picea, T. claibornensis, T. fraudulenta, T. rugosa, T. vultuosa, T. cragini, T. alabamensis,* and *T. neglecta)*, and 5 species were represented by only a single dissection each *(X. occidentalis, T. henriettae, T. discoidea, T. fulciden,* and *T. pendula).* The remaining 25 species were represented by three or more dissections each, usually with at least three from a single population.

A representative dissection was illustrated for 39 of the 40 species, by means of a drawing tube attached to a Zeiss dissecting microscope. Relaxed specimens were used for 35 species, but because of limited material *X. occidentalis, T. complanata, T. obsoleta,* and *T. fallax* were represented by contracted specimens. *T. rugosa* became available too late to be illustrated.

Comparative anatomies of eastern American triodopsine outgroups were available in published illustrations. According to Emberton's (1986) phylogenetic analysis of the Polygyridae, eastern triodopsines are the most primitive group in the family, and their closest outgroups are the western American triodopsine *Vespericola,* and the ashmunellines *Cryptomastix* (western) and *Allogona* (western, with one eastern species: *A. profunda*). Penial-morphological data on these genera were available from Pilsbry (1940) and Webb (1948, 1968, 1970a, 1970b, 1970c). A more distant polygyrid outgroup of the triodopsines is the ashmunelline genus *Ashmunella,* the penial morphology of which was gotten from Pilsbry (1940) and Webb (1954). The closest non-polygyrid outgroups of triodopsines, according to the Emberton (1986) hypothesis, are the Corillidae, Ammonitellidae, and Oreohelicidae. In the Corillidae, only the external, uneverted penial morphology of one species is known (Solem, 1966); in the Ammonitellidae, limited details of the penial sculpture are known for *Polygyrella, Polygyroidea,* and *Ammonitella* (Pilsbry, 1939: figs. 369 #5a, 371 #5a, 373 #1g); in the Oreohelicidae, penial sculpture is known for a number of *Oreohelix* species (Pilsbry, 1939; Solem, 1978b). Another, more distant outgroup to the triodopsines which was considered were the Camaenidae, the penial anatomy of many species of which is known through the work of Wurtz (1955) and Solem (1979, 1981a, 1981b, 1984). See Tillier (1986) for an alternative view on triodopsine outgroups.

Additional methods were used for the study of the *Neohelix albolabris* and *alleni* groups. In order to quantify genitalic differences among taxa, 7 measurements were taken from one dissection per population for three populations each of *N. alleni* (pooling the two subspecies, which did not differ in the measurements taken—see Fig. 3), *N. albolabris albolabris, N. albolabris bogani* Emberton, new subspecies, *N. major,* and *N. solemi.* For these measurements, the most relaxed specimens were chosen from widely distributed populations. The measurements were: (1) the length of the penis, in mm, from its junction with the vagina to the internal apex of the dissection; (2) the number of pilastral lappets (this and other terminology is defined later) per 2.6 mm at the midpoint of the pilaster; (3) the number of columns of wall pustules per 1.3 mm, measuring transversely across the penial wall adjacent to the pilaster about two-thirds of its distance from the internal penial apex; (4) the length of the verge in mm; (5) the maximum width of the pilaster in mm; (6) the distance in mm from the external apex of the penis to the midpoint of the origin of the penial retractor muscle on the vas deferens; and (7) the length of the vas deferens, in mm, from where it bends at the external junction of the penis and vagina to its point of insertion at the external penial apex.

Shell analysis

Phylogenetic analysis to the species-group level was entirely free of consideration of shell morphology. In the systematic reviews, however (Appendices B and C), comparative conchological descriptions are included to allow identification to species group from shells alone. To aid identification, a representative shell for each of 39 species (all but *T. rugosa*) was illustrated in two views: perpendicular to the plane of the aperture, and in the

plane of the aperture while parallel to the axis of rotation. These views were chosen because they simultaneously show as many important shell features as possible, including apertual dentition, apertural dishing, apertural lip thickness, pre-apertural deflection of the body whorl, umbilicus, height, surface striae, and, in a rough way, whorl count. The shell drawings were made using a drawing tube mounted on a Zeiss dissecting microscope. For most species, the illustrated shell was from the same population from which the penial morphology was illustrated.

Shells of the *Neohelix albolabris* and *alleni* groups were studied in much greater detail. Despite a great similarity in the overall aspect of the shells, and an overlap in shell size among the 6 species and subspecies of this group, subtle conchological differences were apparent. In order to quantify these differences and to objectively test their reliability for identifying the taxa, a multivariate discriminant analysis was performed, beginning with a set of 11 measurements on 55 shells from 28 populations. These populations, their species or subspecies, and the identification numbers of the shells measured from each, are listed in the first three columns of Table 6. For each of the six taxa, a set of populations was chosen which appeared to include its full range of shell variation; from each population, all undamaged adult shells were measured if there were no more than three—if there were more than that, the three shells showing extremes in the population's variation were chosen for measurement.

There were 8 shell variables in which the 6 species and subspecies of the *N. albolabris* and *N. alleni* groups appeared to differ: relative spire height (henceforth called RELSPIRE), whorl expansion rate (WHRLEXPN), relative width of the apertural lip (RELLIP), relative size of the baso-columellar lip node (RELNODE), relative degree of pre-apertural deflection of the body whorl (RELDEFL), density of surface striae (STRIAE), color (BROWN), and sheen (GLOSSY). These variables and the method for quantifying each are listed in Table 5. STRIAE was a direct count, BROWN and GLOSSY were rank measurements, and the remaining 5 (RELSPIRE, WHRLEXPN, RELNODE, RELLIP, AND RELDIFL) were ratios of directly measured or calculated distances. The 11 measurements from which the 8 variables were derived are listed as column headings in Table 6.

Electrophoresis

Posterior foot tissues ("snail tails") were excised from field-activated snails and stored in cryogenic vials in liquid nitrogen. Horizontal starch-gel electrophoresis followed methods of Selander *et al.* (1971) and Shaw & Prasad (1970), as modified by Davis et al. (1981). Twelve enzyme systems yielding 16 loci were used: Sordh, Mdh-1 & 2, Me, Icd, Pgd, Gd-1 & 2, Sod-1 & 2, Got-1 & 2, Pgm, Lap, Mpi, and Gpi (see Appendix A). These loci were chosen because they were genetically interpretable, because they represent a diversity of metabolic pathways, and because several of them have a proven heritability (McCracken, 1976, 1980). Deliberately excluded were enzymes that have been shown to be environmentally induced in pulmonates: esterases (Oxford, 1973, 1978), lactate dehydrogenase (Gill, 1978a), acid phosphatase, and alpha-glycerophosphate dehydrogenase (Gill, 1978b). Complete electrophoretic procedures are given in Appendix A.

The electrophoresed material comprised 249 snails from 64 populations representing 35 of the 40 Hubrichtian (1985) species of eastern triodopsines. The 5 species for which tissue samples were lacking were *T. discoidea, T. fallax, T. obsoleta, T. rugosa,* and *T. soelneri.* Three electrophoresed species had incomplete data: *X. fosteri* (missing Gd-1, Gd-2, and Sod-2), *T. fulciden,* and *T. henriettae* (both missing Gd-1 and Gd-2). All other species (32 total) were represented by at least one population with complete data for all 16 loci.

Seventeen species were represented by a single electrophoresed population each *(T. albamensis, T. burchi, X. caroliniensis, T. claibornensis, T. complanata, X. fosteri, T. fraudulenta, T. fulciden, T. henriettae, N. lioderma, T. messana, T. neglecta, T. pendula, T. picea, T. platysayoides, N. solemi* and *T. vannostrandi);* 13 species were represented by two populations each (*T. anteridon, T. cragini, X. denotata, N. dentifera, N. divesta, T. hopetonensis, T. juxtidens, W. multilineata, X. occidentalis, T. palustris, T. tennesseensis,* and *T. vulgata;* four species were represented by three populations each (*N. albolabris, N. major, X. obstricta,* and *T. vultuosa*); one species was represented by 5 populations (*N. alleni*); and one species was represented by 6 populations *(T. tridentata).* Catalogue numbers of the voucher specimens for all electrophoresed populations are given in col-

umn 2 of Table 2, and in Appendices B and C. Of the total 64 populations, 50 had complete electrophoretic data and 14 had missing data for one to 7 loci.

The number of snails electrophoresed per population (Table 2, column 3) ranged from one to 12, with a mean of 3.9 and a standard deviation of 2.5.

The closest outgroup of eastern triodopsines from which comparative material was available was *Allogona profunda* (Say, 1821), of which two populations with sample sizes of 2 and 10 were electrophoresed.

Data analysis

Penial morphology was analyzed cladistically (Hennig, 1966; Eldredge & Cracraft, 1980; Wiley, 1981). A character-state phylogeny was proposed for each character, using criteria reviewed by Emberton (1986), and its polarity was determined by outgroup comparison (e.g., Watrous & Wheeler, 1981). A taxon-by-character-state matrix was prepared using additive binary coding (Farris *et al.*, 1970). Cladograms were generated from this matrix using the Wagner criterion of unrestricted parsimony (Kluge & Farris, 1969; Farris, 1970), using global branch swapping to approach heuristically the most parsimonious set of trees. The PAUP program (Swofford, 1983) was used for computing the trees. These trees were visually compared branch-by-branch, and each discrepancy was resolved based on which combination of convergences and reversals seemed biologically most plausible. The final result of these comparisons was a single, most parsimonious cladogram that was designated the "Anatomy Tree".

Electrophoretic data were analyzed both cladistically and phenetically. Cladistic analysis employed the independent alleles model (Mickevich & Johnson, 1976), by which alleles not present in the outgroup are considered apomorphous. *Mesodon* was used as the outgroup, because it was the only other polygyrid group for which a comparable electrophoretic data set was available (Emberton, 1986). For each eastern-American triodopsine species, the presence or absence of each apomorphous allele was binary-coded. The resulting data matrix was analyzed by PAUP (Swofford, 1983), using global branch swapping to obtain the first 50 trees with equal, maximum parsimony. These trees were then compared branch-by-branch to determine the most frequently occurring configuration of each branch. In this manner, a single maximum-parsimony, consensus cladogram was arrived at, and was designated the "Alleles Tree."

For phenetic treatment, the electrophoretic data set was divided into two subsets, the first consisting of 32 species plus the outgroup *(Allogona profunda)*, each represented by a single population with complete data for all 16 loci. The second subset consisted of three species not included in the first subset, plus additional populations of 18 species in the first subset, plus two outgroups (*A. profunda and Mesodon zaletus* [Binney, 1837]), for a total of 33 populations. In this second subset, all loci with incomplete data were deleted, leaving 8 loci: Sordh, Mdh-1, Mdh-2, Pgd, Sod-1, Got-1, Pgm, and Gpi. For each of the two subsets, Prevosti distances (Wright, 1978) among populations were calculated and subjected to the distance-Wagner procedure (Farris, 1970), with branch-length optimization, using NT-SYS computer programs (Rohlf et al., 1972). The resulting trees were designated the "Wagner-1 Tree" and the "Wagner-2 Tree."

The Anatomy, Alleles, Wagner-1, and Wagner-2 Trees were combined to produce a Consensus Tree in the following manner. Each of the four trees was weighted by a combination of two criteria: the number of data units and the relative reliability of the data units. The data units were considered to be character-state transformations in the Anatomy and the Alleles Trees, and to be alleles in the Wagner-1 and Wagner-2 Trees. The reliability of anatomical data-units relative to allozymic data-units was estimated by dividing the number of convergences and reversals in the Anatomy Tree by the number of convergences and reversals in the Alleles Tree. Multiplying this reliability index times the number of anatomical character-state transformations gave a relative weight for the Anatomy Tree. The relative weight of the Alleles Tree was taken as the number of single-allelic transformations. Relative weights of the Wagner-1 and Wagner-2 Trees were considered to be to the number of alleles comprising the data subset from which each tree was calculated. Using these weightings to resolve conflicts, the four trees were visually compared branch-by-branch to arrive at a Consensus Tree.

For a more detailed cladistic analysis of the *Neohelix albolabris* and *alleni* groups, addi-

tional anatomical character-state transformations were proposed based on the quantitative comparisons in penial morphology. All the available transformations were then used to construct a maximum-parsimony cladogram by hand.

Multivariate discriminant analysis of shells of the *Neohelix albolabris* and *alleni* groups employed SAS software (SAS Institute, 1982). The 6 taxa were discriminated on the basis of 8 shell variables (Table 5). Eight of the 55 measured shells had an incompletely matured apertural lip (Table 6, last column), which affected the values of RELNODE and RELLIP, therefore these shells were deleted from the analysis.

Patterns of genitalic evolution

Patterns of evolution in penial morphology were analyzed by comparing sister taxa (species or species clusters appearing dichotomously in the Consensus Tree). For each of 25 sister taxa, the difference in penial morphology was ranked as great, moderate, slight, or none; and the geographical relationship of their ranges was classified as allopatric, sympatric, parapatric, or peripatric (in which one taxon is a small-ranged endemic peripheral to the much broader range of the other). Geographic ranges were gotten from Hubricht (1985).

The importance of reproductive character displacement was assessed by comparing, for each of 12 species, populations sympatric vs. allopatric with another triodopsine species of similar shell size and shape. Table 9 lists the species, the sympatric species, the localities of compared populations, and the number of dissections per population. Allopatric populations of *T. tridentata* were compared with populations sympatric with *T. vulgata, X. obstricta, T. picea,* and *T. juxtidens;* likewise *T. vulgata* was tested for penial differences due to sympatry with *X. denotata, T. tennesseensis,* and *T. tridentata.* Also tested were *N. albolabris* against *N. alleni* and *N. dentifera; T. juxtidens* against *T. tridentata;* and both *N. alleni* and *N. dentifera* were tested against *N. albolabris.*

Patterns of shell evolution

To analyze conchological evolution at the generic and species-group levels, a representative shell was chosen for each species and was mounted in its proper position on the Consensus Tree. Patterns of change through time were interpreted under the assumptions that (1) the Consensus Tree was an accurate estimate of true phylogeny, and (2) the shell morphology of each (unknown) ancestor was between the morphologies of its extant descendents.

Patterns at the species level were assessed using Vagvolgyi's (1968) conchological monograph, in which the ranges of basic shell measurements and ratios are listed within each species description. Vagvolgyi's total data base comprises 31,269 shells from 556 museum lots. For the present analysis, his data were compiled into tabular form, and a "diameter range" index (Solem, 1981a) was calculated for each species: the greatest minus the least measured shell diameter, divided by the least, and expressed as a percent.

TAXONOMIC HISTORY

Triodopsis and *Xolotrema* were erected by Rafinesque in 1819 to separate *tridentata, denotata,* and other tridentate North American species from *Helix,* then a massive genus comprising most of the world's land snails. The new generic names were largely ignored, however (all polygyrids going by the name *Polygyra* Say, 1818), until "Tryon (1867), Binney & Bland (1869), and later authors, following von Martens (1860) used *Triodopsis* for all of the depressed, two- or three-toothed [land shells] of the eastern United States, and *Mesodon* for the more capacious, subglobose species with a small parietal tooth, or toothless [and thus abandoned the name *Xolotrema*]" (Pilsbry, 1940). Many authors (e.g., Simpson, 1901; F. C. Baker, 1939) continued, however, to synonyomize *Triodopsis* and *Mesodon* under the blanket genus *Polygyra.* It wasn't until Pilsbry's (1940) monograph on North American land snails that *Triodopsis* was clearly characterized anatomically, was distinguished anatomically from *Mesodon,* and was recognized as covering most of the wide range of shell shapes also covered by *Mesodon* but formerly erroneously divided between the two genera.

In this monograph, Pilsbry (1940) divided *Triodopsis* into the four subgenera *Triodopsis s. str.* Rafinesque, 1819; *Cryptomastix* Pilsbry, 1939; *Xolotrema* Rafinesque, 1819 (bringing this name back from obscurity); and

Neohelix von Ihering, 1892, based on shell shape and reproductive anatomy, with *Cryptomastix* disjunct in the Pacific Northwest. Pilsbry's taxonomy of eastern *Triodopsis* (i.e., the eastern triodopsines) was almost exclusively based on shell morphology, despite the fact that he illustrated the reproductive systems of several species. He recommended that future revisions make use of penial morphology.

Additional species and subspecies of *Triodopsis* were subsequently described by Lutz (1950) and Hubricht (1950, 1952, 1958). A summary of new and emended taxa from 1948 to 1984 was provided by Miller *et al.* (1984).

Webb (1947a, 1947b, 1948, 1952, 1954, 1959) published a series of reports on the reproductive behavior and anatomy of selected species of triodopsines, and pointed out—as Pilsbry had predicted—important variation in penial sculpture, upon which he based several taxonomic changes. In his 1952 paper, Webb elevated *Xolotrema* to a full genus (defined as possessing a penial verge) and transferred the subgenus *Neohelix* to it. In 1954, Webb elevated the Pacific Northwestern subgenus *Cryptomastix* to generic level within the new subfamily *Ashmunellinae,* thereby restricting *Triodopsis* to eastern North America. Also based on penial morphology, Webb erected the subgenus *Wilcoxorbis* for *Xolotrema fosteri* (Webb, 1952), the subgenus *Haroldorbis* for *Triodopsis cragini,* and the section *Shelfordorbis* for *Triodopsis vulgata* (Webb, 1959).

Vagvolgyi's (1968) monograph, "Systematics and Evolution of the Genus *Triodopsis* (Mollusca: Pulmonata: Polygyridae)", summarized a massive amount of new data on conchological variation. This revision was based solely on shells and ignored Webb's (1947–1961) anatomical work and validly proposed supraspecific taxa (see Grimm, 1975; Solem, 1976). Additional shortcomings of this work were that (1) the numerical formulae used for separating and defining taxa were arbitrary, based on neither multivariate nor any other objective criterion; (2) designation of "hybrids" was based on the untested criterion of high within-populational variation, the presence of which can have other explanations; and (3) the ecological descriptions were often arrived at by comparing species ranges with broad-scale vegetation maps, thereby sometimes missing important finer-grained ecological differences (L. Hubricht, personal communication; personal observations).

Vagvolgyi's *Triodopsis copei* (Wetherby) was subsequently split into the three species *cragini, vultuosa,* and *henriettae* by Cheatum & Fullington (1971) in their monograph of Texas polygyrids.

Grimm (1975) gave brief comparative descriptions of *Triodopsis* and its species groups, and summarized his systematic conclusions concerning the *T. fallax* group based on a ten-year study of geographic shell variation, laboratory hybridization, and, to lesser extent, penial morphology. Grimm's conclusions based on these (largely undocumented) studies were concordant with those earlier postulated from geographic shell variation by Hubricht (1953), but ran counter to those of Vagvolgyi (1968).

Solem's (1976) "Comments on Eastern North American Polygyridae" compared the sympatric, conchologically similar *Neohelix divesta* and *N. albolabris* with each other and with three sympatric, conchologically similar species of *Mesodon* in shell, radular structure, jaw structure, external aspect of the reproductive system, and dissected penial morphology. Comparative data on the rare *Triodopsis platysayoides* were also included. Solem emphasized the need for sympatric-species comparisons to establish criteria for distinguishing allopatric species, and showed through adequate illustrations that penial morphology was an even richer source of systematically useful characters than Webb's illustrations had indicated.

McCracken & Brussard's (1980) study of electrophoretic variation among populations of the "white-lipped land snail", although incorrect in many of its conclusions due to taxonomic errors (Emberton, McCracken, & Wooden, in preparation), showed the presence of significant allozymic variation within *Neohelix* and demonstrated the heritability of several loci in a New York population of *N. albolabris.*

Emberton (1985) dissected a temporal series of *Triodopsis tridentata* and found that extreme seasonal variation ruled out reproductive-organ volume and, to some extent, organ length as useful systematic characters for triodopsines.

Hubricht's (1985) book of range maps and ecological sketches of eastern North American land snails discarded most of Vagvolgyi's (1968) species-level taxonomic changes and elevated several of Pilsbry's (1940) subspe-

cies and the one subspecies of Lutz (1950) to full species, resulting in 40 total species; taxonomy between the genus and species levels was not included. Richardson's (1986) bibliographic catalog of polygyrid species did not incoprorate Hubricht's (1985) changes.

GENITALIC ANALYSIS

Variation

The eastern-triodopsine penis and its major structural features are presented diagrammatically in Fig. 1. The uneverted penis is held internally by a single retractor muscle attached to the vas deferens near the penial apex. The penial tube varies from short to extremely long, from cylindrical to clubbed. The position of entry of the vas deferens at the ejaculatory pore varies from terminal to subterminal. The collar-like muscular sheath, which circularly attaches to the basal penis and connects to the vas deferens via the retentor muscle, varies from short (covering only the basal fourth of the penis) to very long (covering the entire penis).

Dissection of the uneverted penial tube reveals its ornately sculpted functional surface (Fig. 1). The dorsal pilaster is a longitudinal outgrowth of the penial wall; it varies among species in both length and surface sculpture. The penial wall (exclusive of the dorsal pilaster) is covered with rows of pustules. These pustules vary in size and shape among species, and are sometimes lacking. The pustular rows vary in pattern; when their pustules are absent they appear as low, smooth ridges. The area surrounding the ejaculatory pore may be flat or may be elongated as a flap-like, conical verge of variable size and shape. Other features which also may be present (but are not shown in Fig. 1) are a smooth ventral sperm groove; a fleshy, knob-like peduncle beneath the ejaculatory pore; and a low ventral pilaster.

Proximal to the upper, sculpted region of the penis lies the basal penis. This region is smooth, lacking pustules. Its walls vary from thin with random folds, to thick and muscular with regular folds produced by both longitudinal and circular muscle bands. Proximal to the basal penis, between the vaginal opening and the genital pore, is the atrium. The wall of this region is always smooth and thin, bearing random folds.

Variation within any given population was minor in sculptural details, but major in such elastic features as penis length, sheath length, retractor-muscle and retentor-muscle lengths, and the configuration of folds in the basal penis. Much of this variation seemed to correlate with the contractile condition of the specimen.

Seasonal variation in penial morphology in the studied population of *Triodopsis tridentata* was slight. The post-mating snail had a thinner wall, and its pustules were somewhat thin and flap-like compared to the more prominent, robust pustules of both mating-ready snails. The distribution and relative sizes of the pustules, however, remained constant.

In all 13 species for which more than one population was dissected, upper penial sculpture was remarkably uniform. An example of this geographic stability is illustrated in Fig. 3, which shows the penial morphologies of two populations of *Neohelix alleni* separated by the Mississippi River Valley. Judging both from the wide range disjunction of this species (Fig. 49) and from the fossil-palynological evidence concerning its deciduous-forest habitat (Delcourt & Delcourt, 1981), these two populations had been genetically isolated for at least 20,000 years, which is probably equivalent to at least half as many generations (see McCracken, 1976). Nevertheless, these populations had accumulated only minor differences in penial sculpture: the eastern population *(N. alleni fuscolabris)* differed from the western *(N. alleni alleni)* only in its somewhat larger verge and in having its pustulose region descend approximately 20% lower.

Because of this general morphological conservatism, the penial morphology of each species could be adequately represented by a single illustration (Figs. 2–18).The only species not illustrated *(Triodopsis rugosa)* was very similar to *T. fulciden* (Fig. 18b).

Descriptions

Measurements in the following descriptions were taken solely from the illustrations (Figs. 2–18) and do not in any way reflect natural variation. Penis length was measured from the apex to the genital pore. The verge was measured from its dorsal side. The terms "large", "small", etc. are used relative to total penis length.

Neohelix albolabris (Say, 1816)—Dissections: 27 from 14 populations. Fig. 2d-g. Length 17 mm. Shape cylindrical, the apical

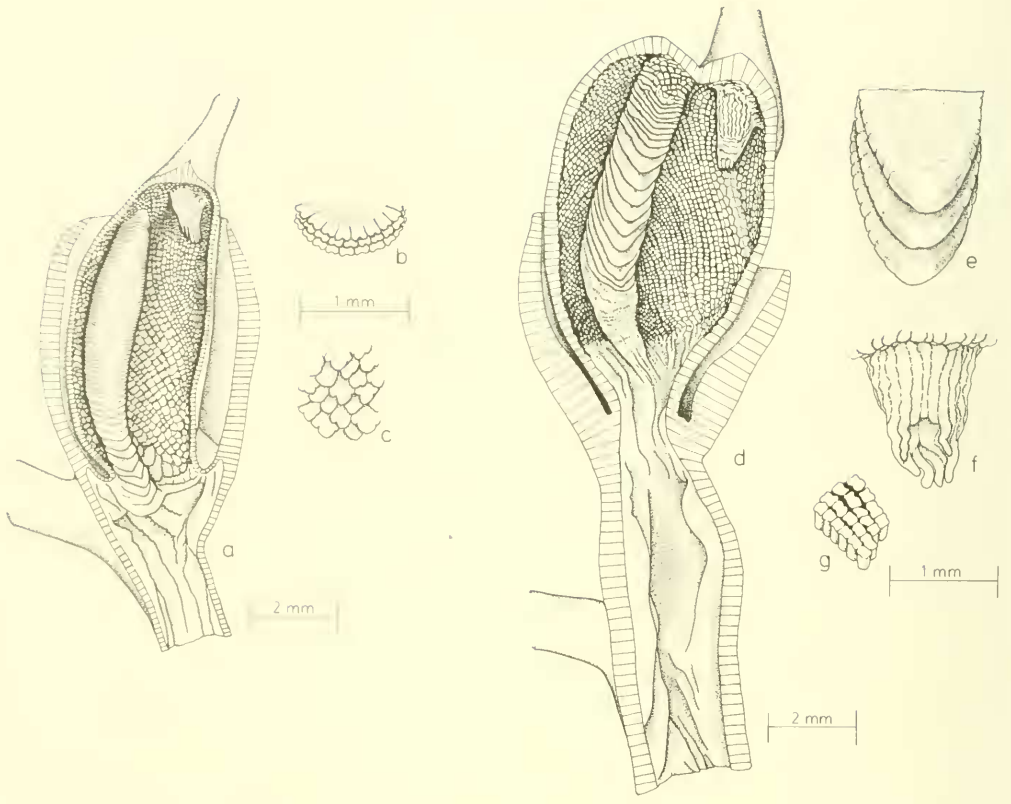

FIG. 2. Opened uneverted penial tubes. **a.** *Neohelix dentifera* (Binney, 1837). FMNH 214810 #8 (also dissected #1, 4; FMNH 214809 [sympatric with *Neohelix albolabris*] #2, 7, 14). **b.** Diagrammatic detail of 3 lappets from center of pilaster of a, showing substructure of pustules. **c.** Diagrammatic detail of central wall pustules of a, showing lateral cusps. **d.** *Neohelix albolabris* (Say, 1816). FMNH 214920 (sympatric with *Neohelix dentifera*) #14 (also dissected #9, 11, 17; and 8 other populations——see Appendix B). **e.** Detail of 3 lappets from center of pilaster of d, showing substructure of apparently fused pustules. **f.** Detail of other side of verge in d, showing opening of vas deferens. **g.** Detail of wall pustules of d.

half enlarged. Ejaculatory pore terminal, on a verge. Verge large (length 1.5 mm), terminal, dorso-laterally compressed, back-pointing, with a ventrally subterminal pore and sculpted with surface cords continuing into about 6 terminal papillae (Fig. 2f). Dorsal pilaster long (7 mm) and broad (mid-width 1.3 mm), and superficially resembling a stack of tongue-like lappets with edges slightly convex and regularly marked with slight indentations (Fig. 2e). Basal half of the penis smooth with random folds; upper half uniformly sculpted with 25–35 adjacent, generally unmerging, equilateral columns of distinct, equal-sized pustules (Fig. 2g), radiating from the pore region. Sheath enclosing less than half of the upper, sculpted region of the penis.

Neohelix alleni (Sampson, 1883)—Dissections: 15 from 8 populations. Fig. 3. Length 20 mm. Shape cylindrical, the apical half enlarged. Ejaculatory pore terminal, on a verge. Verge relatively large (1.0 mm), terminal, dorso-laterally compressed, back-pointing, with a ventrally subterminal pore and sculpted with surface cords continuing into about 8 terminal papillae (Fig. 3b). Dorsal pilaster long (11 mm) and broad (mid-width 1.4 mm), and superficially resembling a stack of tightly appressed tongue-like lappets with smooth edges. Basal one-fourth to one-third of the penis smooth with random folds; upper half uniformly sculpted with 25–35 adjacent, generally unmerging, equilateral columns of distinct, equal-sized pus-

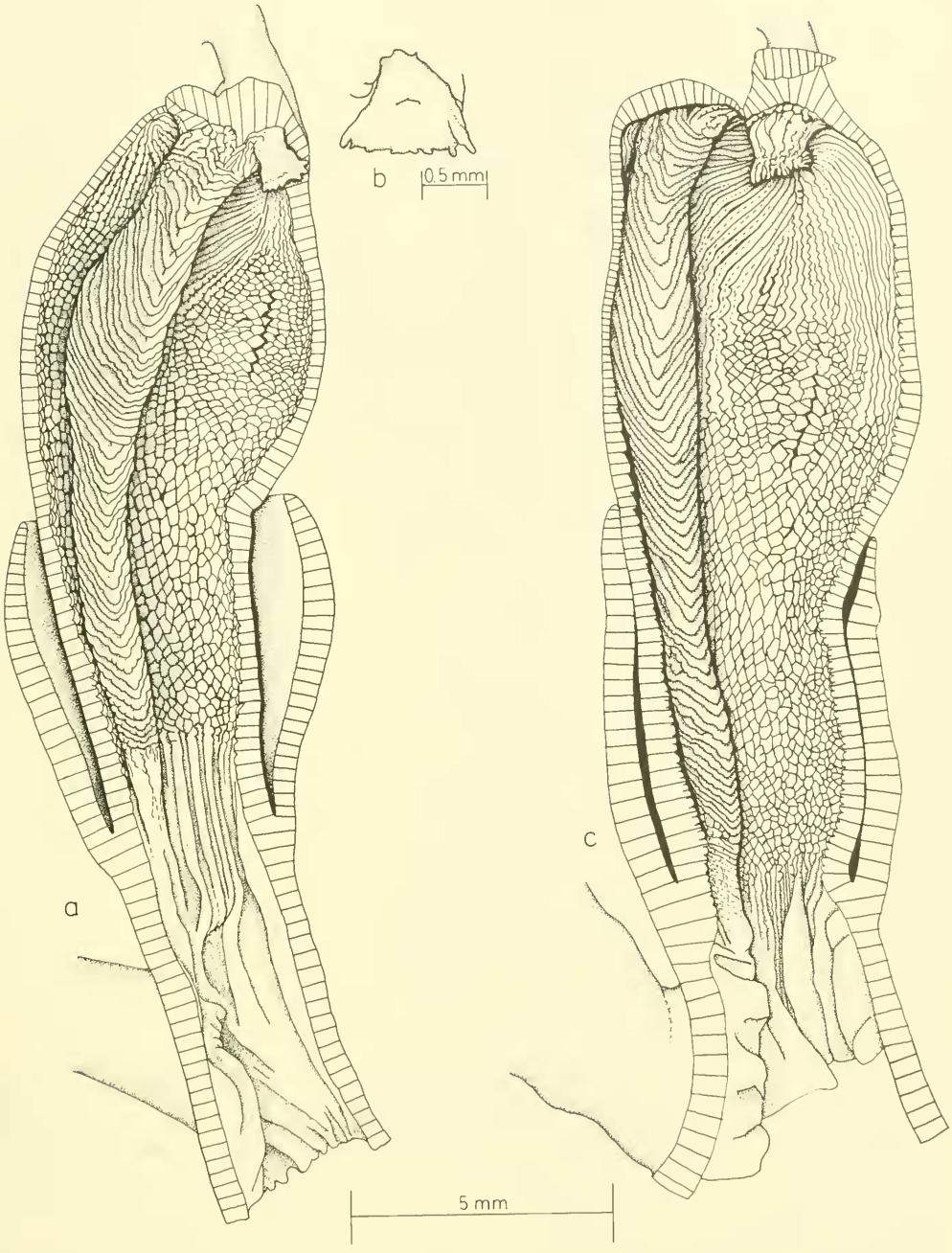

FIG. 3. Opened uneverted penial tubes. **a.** *Neohelix alleni alleni* (Sampson, 1883). FMNH 214911 #12 (also dissected #11, 13; and 7 other populations—see Appendix B). **b.** Reverse side of verge of a, showing opening of vas deferens. **c.** *Neohelix alleni fuscolabris* (Pilsbry, 1903). FMNH uncat. #1 (also dissected #2; FMNH uncat. #7, 11, 15). These two subspecies have probably been separated by the Mississippi River Valley for at least 20,000 years but show little difference in penial morphology.

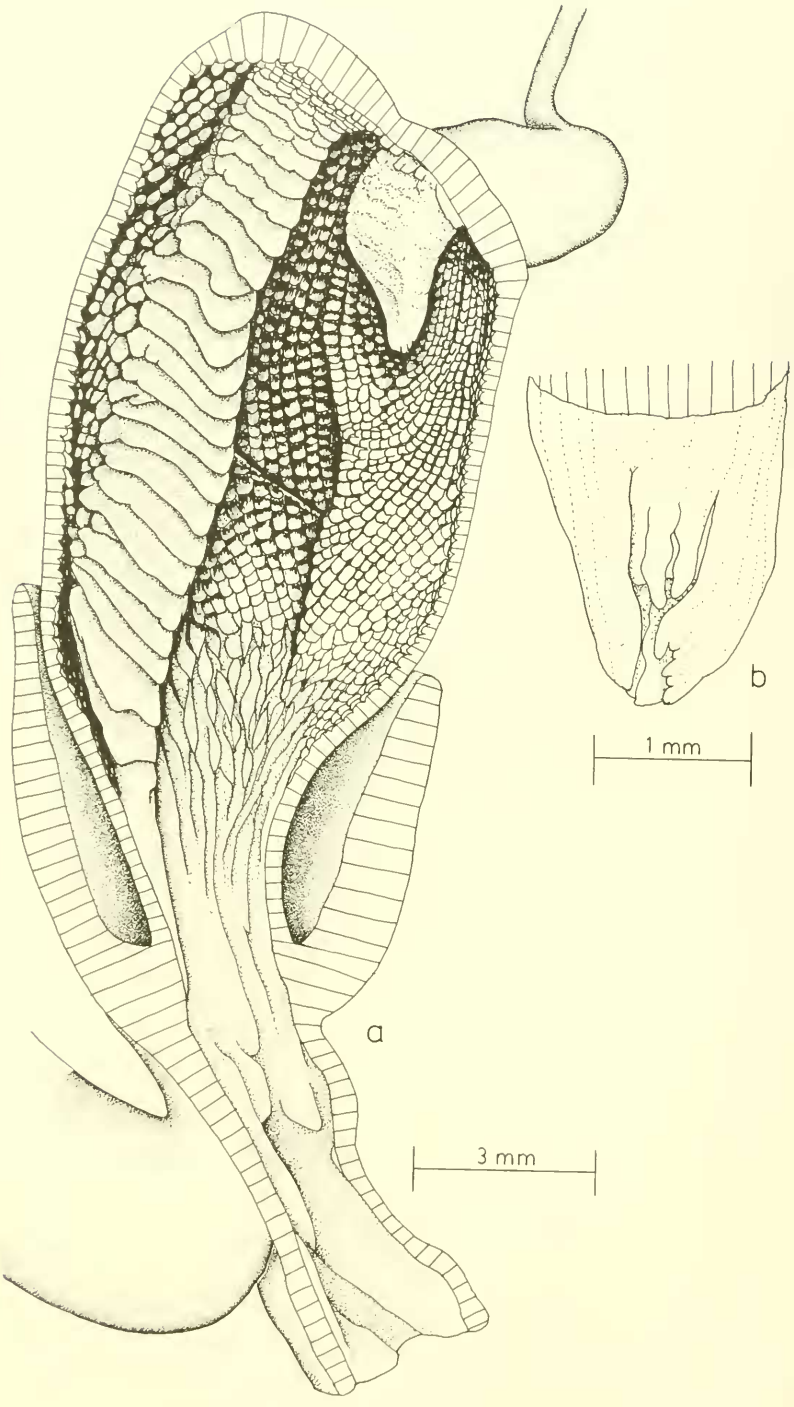

FIG. 4. Opened uneverted penial tube. **a.** *Neohelix major* (Binney, 1837). FMNH 214930 #6 (also dissected #7, 8; and other populations—see systematic section). **b.** Detail of the reverse side of verge of a, showing opening of vas deferens.

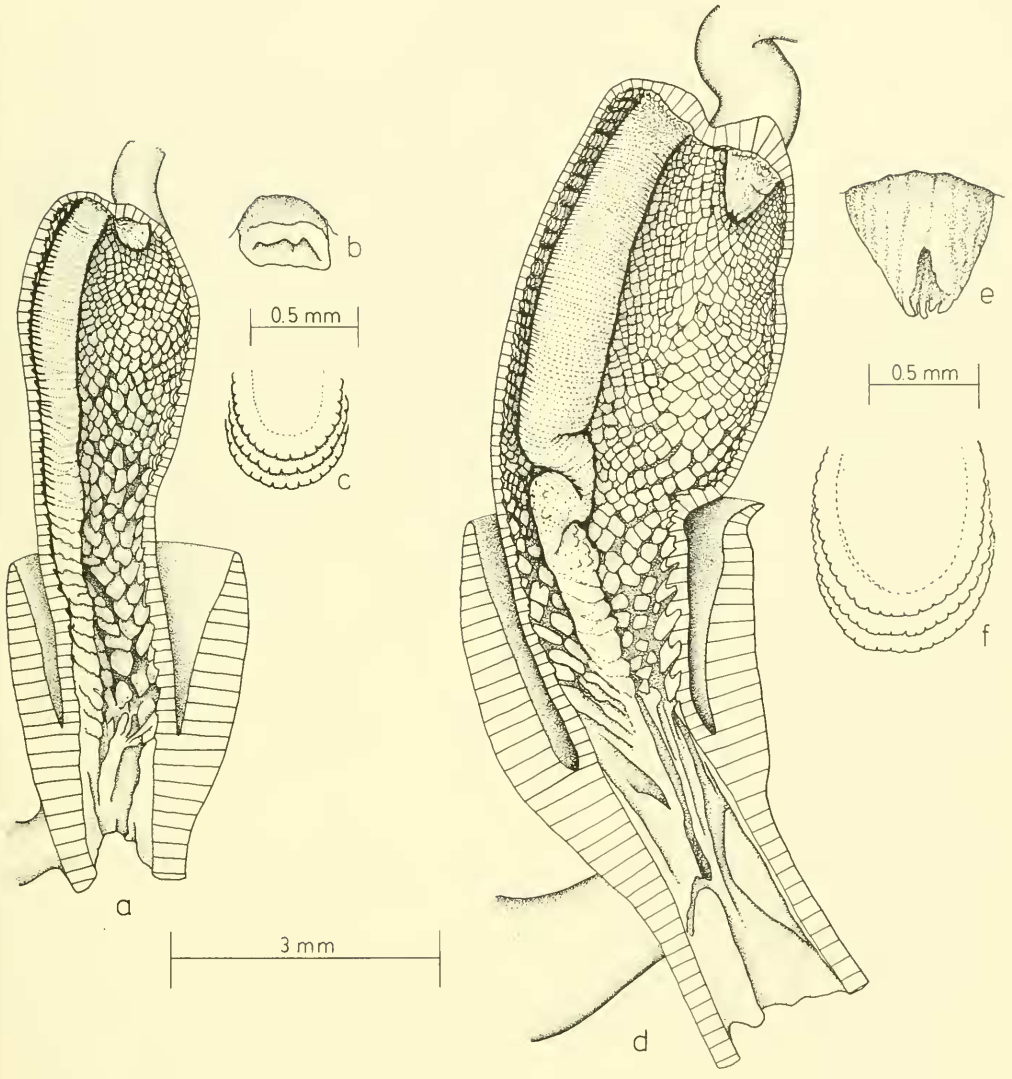

FIG. 5. Opened uneverted penial tubes. **a.** *Neohelix lioderma* (Pilsbry, 1902). FMNH 214844 #A (also dissected #9 and #B, C). **b.** Reverse of verge of a, showing opening of vas deferens. **c.** Detail of 3 lappets from center of pilaster of a, showing substructure suggesting laterally fused pustule. **d.** *Neohelix divesta* (Gould, 1848). FMNH 214813 #1 (also dissected #7, 8, 10; FMNH 176089). **e.** Reverse of verge of d, showing opening of vas deferens. **f.** Detail of 3 central lappets of pilaster of d, showing substructure suggesting laterally fused pustules.

tules radiating from the pore region. Sheath enclosing less than half of the upper, sculpted region of the penis.

Neohelix dentifera (Binney, 1837)—Dissections: 6 from 2 populations. Fig. 2a-c. Length 12 mm. Shape cylindrical, the apical half enlarged. Ejaculatory pore terminal, on a verge. Verge moderate in size (length 0.9 mm), terminal, dorso-laterally compressed, back-pointing, with a ventrally subterminal pore and sculpted with surface cords continuing into about 6 terminal papillae. Dorsal pilaster long (7 mm) and broad (mid-width mm), and superficially resembling a stack of thin, plate-like lappets with edges comprised

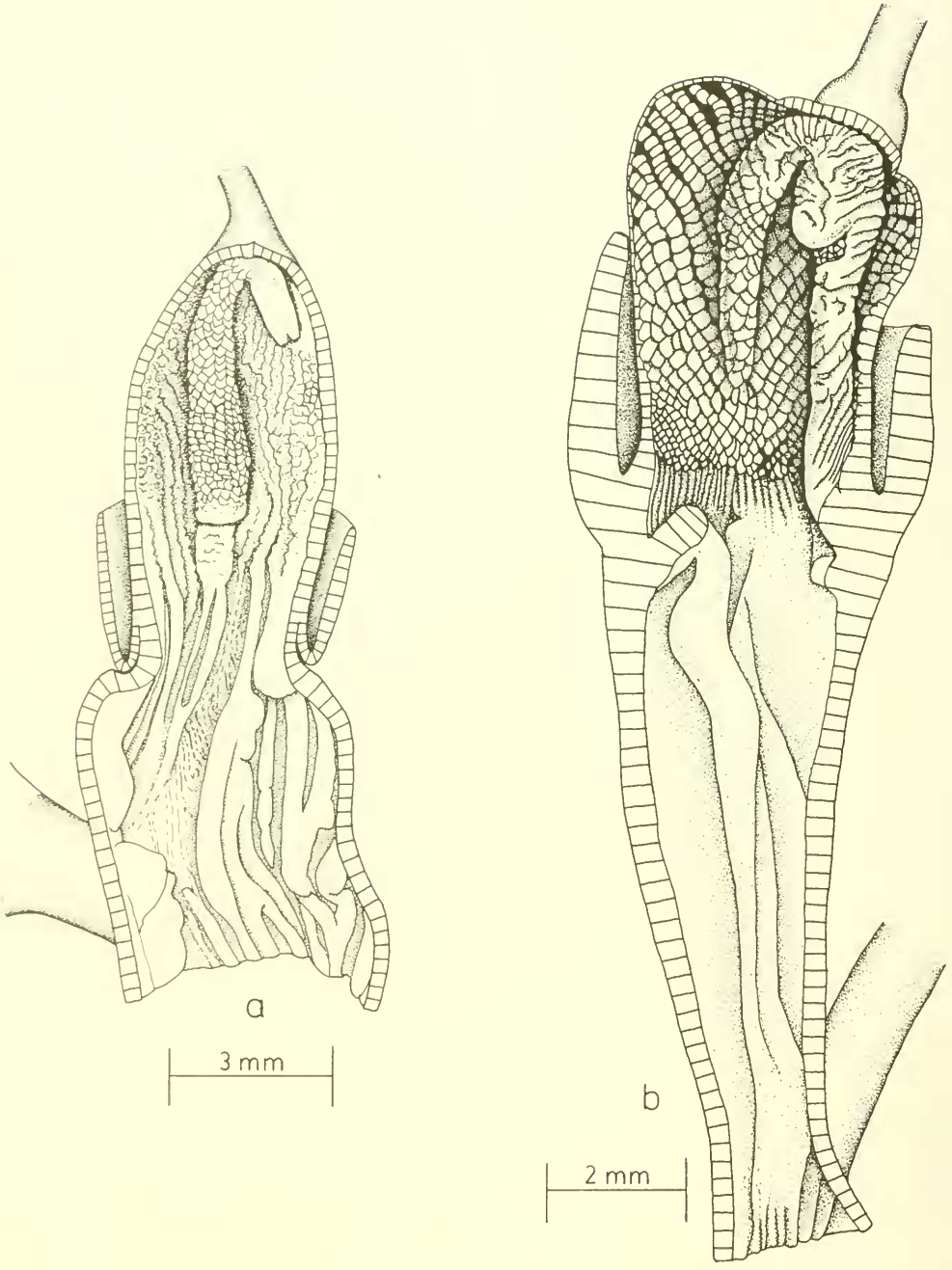

FIG. 6. Opened uneverted penial tubes. **a.** *Webbhelix multilineata* (Say, 1821). FMNH 214848 #2 (also dissected FMNH 214849 #1, 5, A; Hubricht 48600 #A, B, C). **b.** *Neohelix solemi* Emberton, new species. FMNH 214936 #1 (also dissected 13 other populations—see Appendix B).

of equal, bi-lobed units (Fig. 2b). Basal one-fourth of the penis smooth with random folds; upper half uniformly sculpted with 25–35 adjacent, generally unmerging, equilateral columns of distinct, approximately equal-sized, lobed pustules (Fig. 2c), radiating from the

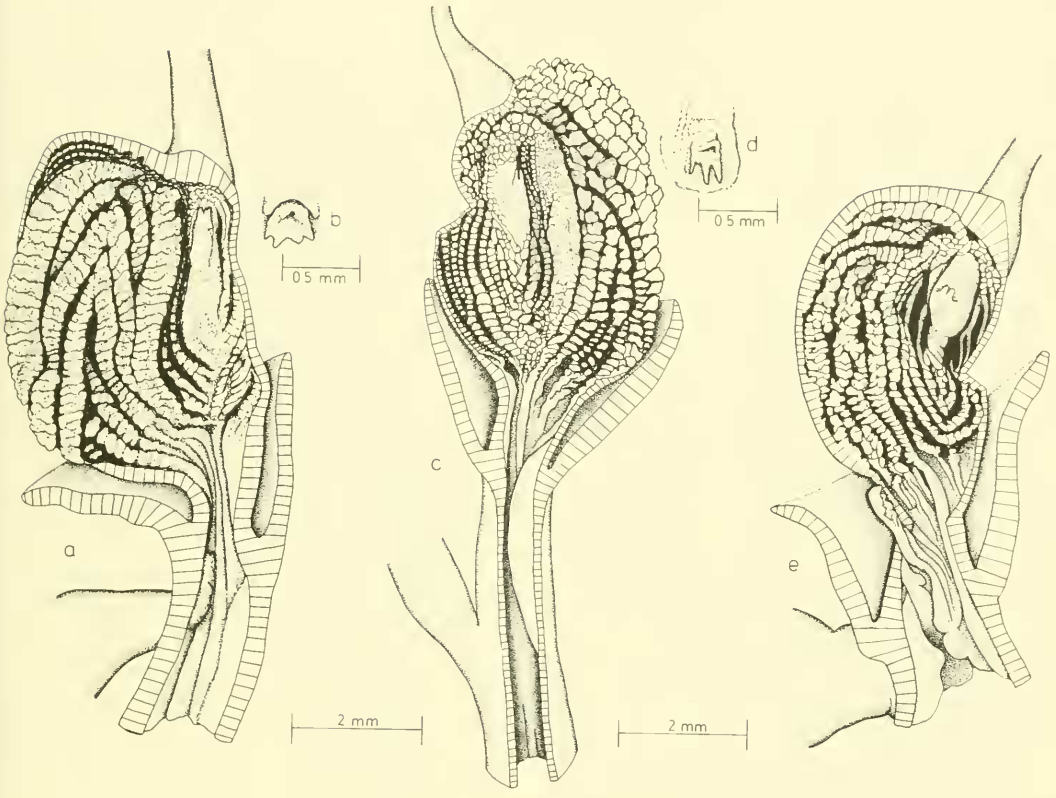

FIG. 7. Opened uneverted penial tubes. **a.** *Xolotrema denotata* (Férussac, 1821). FMNH 214806 #6 (also dissected #1, 2). **b.** Reverse of verge of a. **c.** *Xolotrema obstricta* (Say, 1821). FMNH 214854 #9 (also dissected #1). **d.** Reverse of verge of c. **e.** *Xolotrema caroliniensis* (Lea, 1834). FMNH 171142 #A (also dissected #B).

pore region. Sheath enclosing one half to two-thirds of the upper, sculpted region of the penis.

Neohelix divesta (Gould, 1848)—Dissections: 4 from 1 population. Fig. 5d-f. Length 10 mm. Shape cylindrical, the apical half enlarged. Ejaculatory pore terminal, on a verge. Verge moderate in size (length 0.6 mm), terminal, dorso-laterally compressed, back-pointing, with a ventrally subterminal pore and sculpted with surface cords continuing into about 6 terminal papillae (Fig. 5e). Dorsal pilaster long (7 mm) and broad (mid-width 0.8 mm), and superficially resembling a stack of thin, plate-like lappets with regularly indented edges (Fig. 5f). Basal one-fourth of the penis smooth with random folds; upper half uniformly sculpted with 25–35 adjacent, generally unmerging, equilateral columns of distinct, approximately equal-sized, lobed pustules, radiating from the pore region. Sheath enclosing less than half of the upper, sculpted region of the penis.

Neohelix lioderma (Pilsbry, 1902)—Dissections: 4 from 1 population. Fig. 5a–c. Length 7 mm. Shape cylindrical, the apical half enlarged. Ejaculatory pore terminal, on a verge. Verge (shown partially inverted in Fig. 5a–b) moderate in size (0.3 mm), terminal, dorso-laterally compressed, back-pointing, with a ventrally subterminal pore and sculpted with surface cords continuing into about 6 terminal papillae (not visible in Fig. 5b). Dorsal pilaster long (6 mm) and broad (mid-width 0.5 mm), and superficially resembling a stack of thin, plate-like lappets with regularly indented edges (Fig. 5c). Basal one-fourth of the penis smooth with random folds; upper half uniformly sculpted with 25–35 adjacent, generally unmerging, equilateral columns of

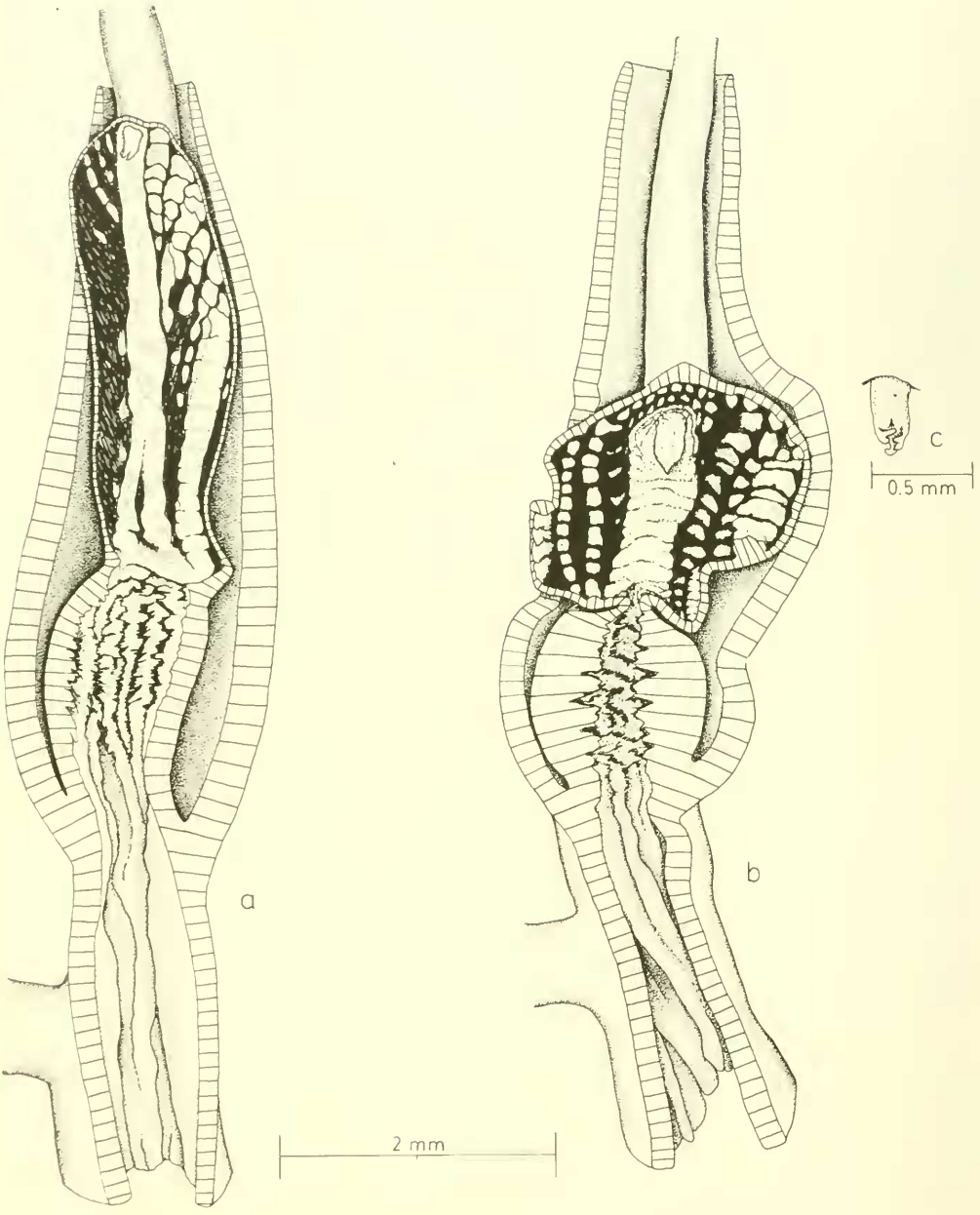

FIG. 8. Opened uneverted penial tubes. **a.** *Xolotrema fosteri* (F. C. Baker, 1932). FMNH 214817 #A (also dissected #B, C, D, E; FMNH 214819 #19). **b.** *Xolotrema occidentalis* (Pilsbry & Ferriss, 1907). FMNH 214856 #5. **c.** Reverse side of verge of b, showing opening of vas deferens.

distinct, approximately equal-sized, lobed pustules, radiating from the pore region. Sheath enclosing less than half of the upper, sculpted region of the penis.

Neohelix major (Binney, 1837)—Dissections: 10 from 5 populations. Fig. 4. Length: 23 mm. Shape cylindrical, the apical half enlarged. Ejaculatory pore terminal, on a

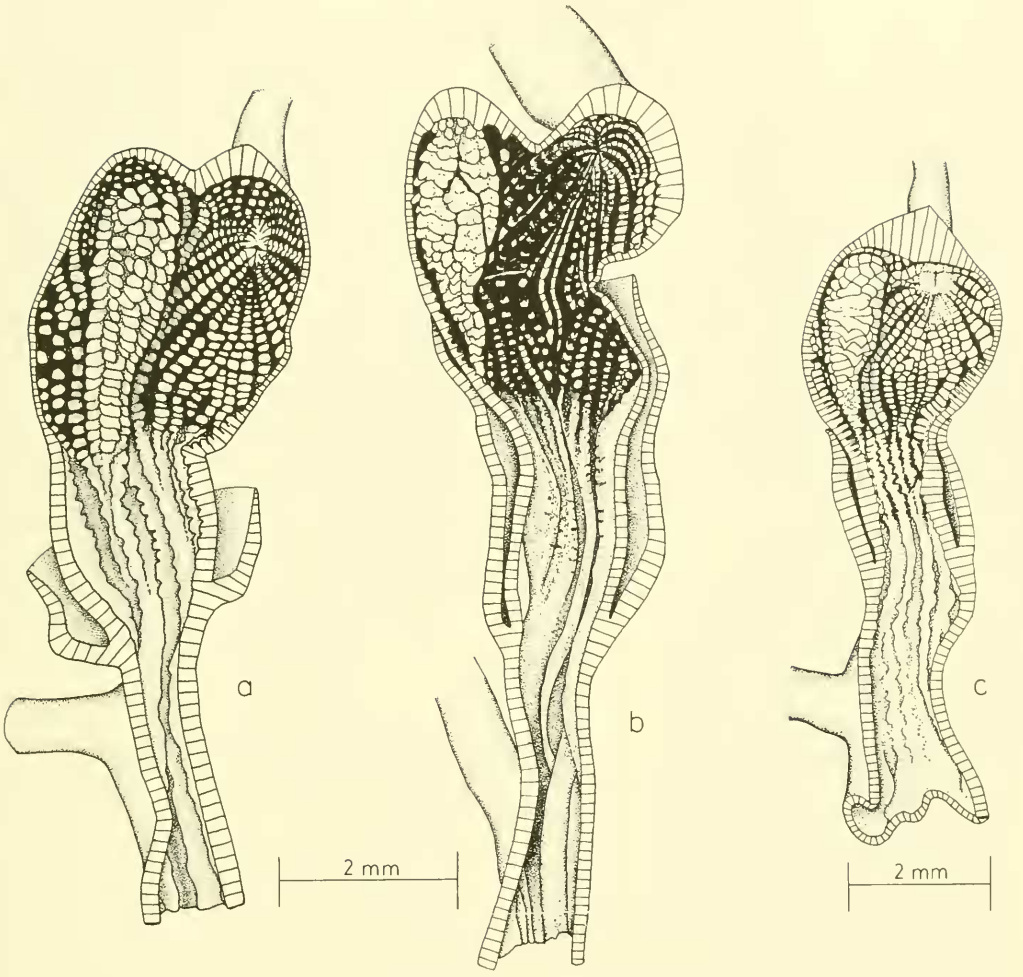

FIG. 9. Opened uneverted penial tubes. **a.** *Triodopsis vulgata* Pilsbry, 1940. FMNH 214884 #1 (also dissected FMNH 214883 #2, 3; FMNH 214885 #1, 2, 3, 4). **b.** *Triodopsis picea* Hubricht, 1958. FMNH 214860 #14 (also dissected #4). **c.** *Triodopsis claibornensis* Lutz, 1950. FMNH 214800 #18 (also dissected #5: has broader pilaster).

verge. Verge very large (length 3.0 mm), terminal, dorso-laterally compressed, backpointing, with a ventrally subterminal pore and sculpted with surface cords continuing into about 12 terminal papillae (Fig. 2b). Dorsal pilaster long (12 mm) and broad (mid-width 2.2 mm), and superficially resembling a stack of tongue-like lappets with edges pronouncedly convex and irregularly wavy, with no regularly-spaced indentations. Basal half of the penis smooth with random folds; upper half uniformly sculpted with 25–35 adjacent, generally unmerging, equilateral columns of distinct, equal-sized pustules radiating from the pore region. Sheath enclosing less than half of the upper, sculpted region of the penis.

Neohelix solemi Emberton, new species—Dissections: 24 from 13 populations. Fig. 6b. Length: 17 mm. Shape cylindrical, the apical half enlarged. Ejaculatory pore dorsally subterminal, on a tiny verge which lies on the apex of a thick, fleshy protuberance. Verge minute (length 0.1 mm), dorso-laterally compressed, backpointing, with a ventrally subterminal pore and sculpted with surface cords continuing into 6–8 terminal papillae. Dorsal pilaster relatively short (3 mm) and narrow (mid-width 0.5 mm), merging terminally with

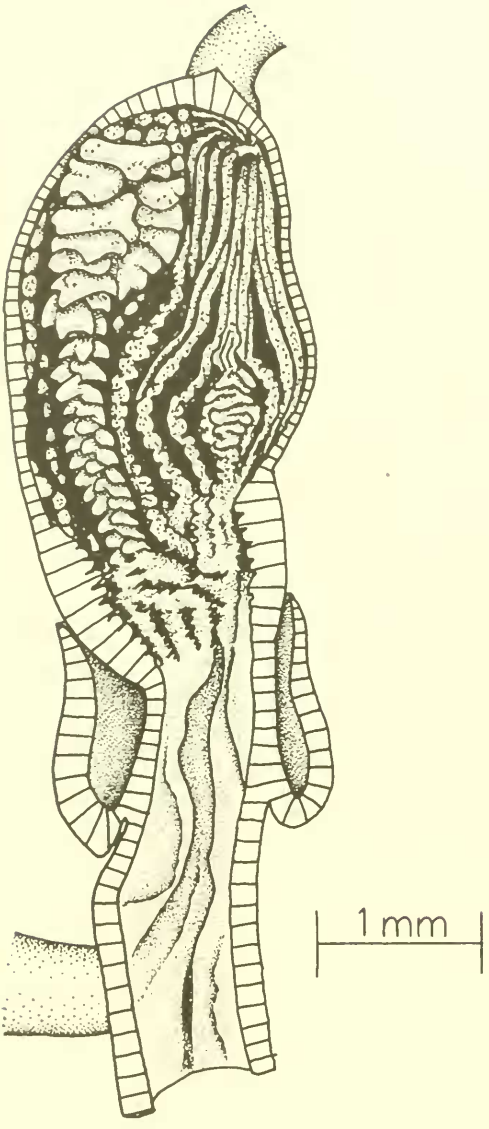

FIG. 10. Opened uneverted penial tube. *Triodopsis fraudulenta* (Pilsbry, 1894). FMNH 214822 #6 (also dissected #8: has more and smaller parts in thickest part of pilaster, with wall pustules more pronounced).

the fleshy protuberance, and superficially resembling an indistinct stack of indistinct tongue-like lappets with variously shaped edges. Ventral wall bearing one to three fold-like pilasters, sculptured no differently than the adjacent penial wall. Basal three-fifths of the penis smooth with random folds; upper two-fifths uniformly sculpted with 25–35 adjacent, generally unmerging, equilateral columns of distinct, equal-sized pustules radiating from the pore region. Sheath enclosing less than half of the upper, sculpted region of the penis.

Triodopsis alabamensis (Pilsbry, 1902)—Dissections: 2 from 1 population. Fig. 16a. Length: 7 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, one-fourth-way from the apex in the upper, sculpted region. Verge absent. A small, smooth, fleshy peduncle present just beneath the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (1 mm) and tapered proximally (mid-width 0.4 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fourth of the penis smooth with random folds; middle fourth with slight circular corrugations; upper half sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing only the basal half of the penis.

Triodopsis anteridon (Pilsbry, 1940)—Dissections: 3 from 2 populations. Fig. 14b. Length: 7 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, one-fourth-way from the apex in the upper, sculpted region. Verge absent. A small, smooth, fleshy peduncle present just beneath the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (1.5 mm) and tapered proximally (mid-width 0.6 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fourth of the penis smooth with random folds; middle fourth with slight circular corrugations; upper half sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing only the basal half of the penis.

Triodopsis burchi Hubricht, 1950—Dissections: 3 from 1 population. Fig. 11a. Length: 8 mm. Shape like a baseball bat. Ejaculatory pore terminal. Verge absent. Dorsal pilaster long (3 mm) and broad (mid-width 1.4 mm), consisting of abutting, unequaly-sized polygons, each covered with knob-like pustules about twice as large as the wall-pustules. Basal half of the penis smooth with random folds and slight circular corrugations; upper half sculpted with 15–20 columns of

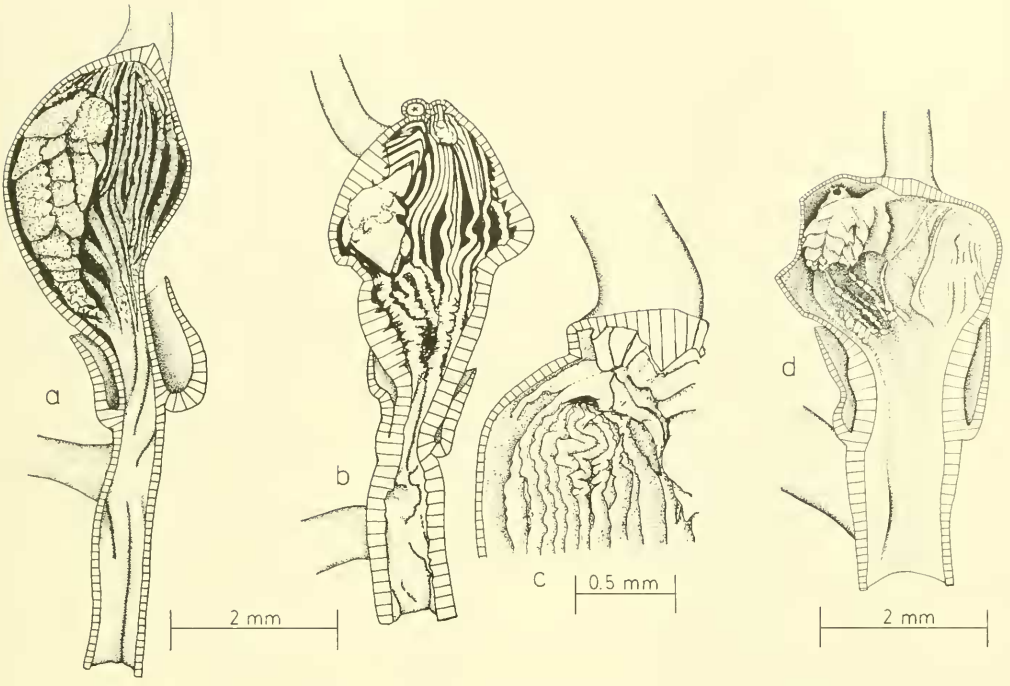

FIG. 11. Opened uneverted penial tubes. **a.** *Triodopsis burchi* Hubricht, 1950. FMNH 214797 #3 (also dissected #5, 12). **b.–c.** *Triodopsis tennesseensis* (Walker & Pilsbry, 1902). **b.** FMNH 214864 #15 (also dissected #13, 14). **c.** Area around opening of vas deferens in #14, showing lack of verge. **d.** *Triodopsis complanata* (Pilsbry, 1898). Hubricht 17932 #C (also dissected #A, B).

equal-sized pustules radiating directly from the pore, the ventral-most columns with pustules indistinct, appearing almost smooth. Sheath enclosing less than half of the upper, sculpted region of the penis.

Triodopsis claibornensis Lutz, 1950—Dissected 2 from 1 population. Fig. 9c. Length: 8 mm. Shape like a baseball bat. Ejaculatory pore ventrally subterminal, about one-fifth-way from the penial apex in the upper, sculpted region. Verge absent. Dorsal pilaster long (2.3 mm) and broad (mid-width 0.8 mm), covered with knob-like pustules all about twice as large as the wall-pustules. Basal half of the penis smooth with random folds and slight circular corrugations; upper half sculpted with 15–20 columns of distinct, equal-sized pustules radiating directly from the pore. Sheath enclosing less than half of the upper, sculpted region of the penis.

Triodopsis complanata (Pilsbry, 1898)—Dissections: 3 from 1 population. Fig. 11d (a contracted specimen). Length: 5 mm. Shape like a baseball bat. Ejaculatory pore terminal. Verge absent. Dorsal pilaster short (1 mm) and broad (mid-width 0.8 mm), consisting of a solid mass bearing three tiers of long, sharp spurs. Basal third of the penis smooth with random folds and slight circular corrupations; upper two-thirds sculpted with 15–20 columns radiating directly from the pore, the dorsal columns bearing indistinct, equal-sized pustules, and the ventral columns completely smooth. Sheath enclosing less than half of the upper, sculpted region of the penis.

Triodopsis cragini Call, 1886—Dissections: 2 from 1 population. Fig. 13b. Length: 8 mm. Shape like a needle. Ejaculatory pore terminal. Verge absent. Dorsal pilaster two-thirds the length of the sculpted region of the penis (2 mm) and tapered proximally (mid-width 0.3 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal third of the penis smooth with random folds; middle third with slight circular corrugations; upper third sculpted with equilateral, widely sepa-

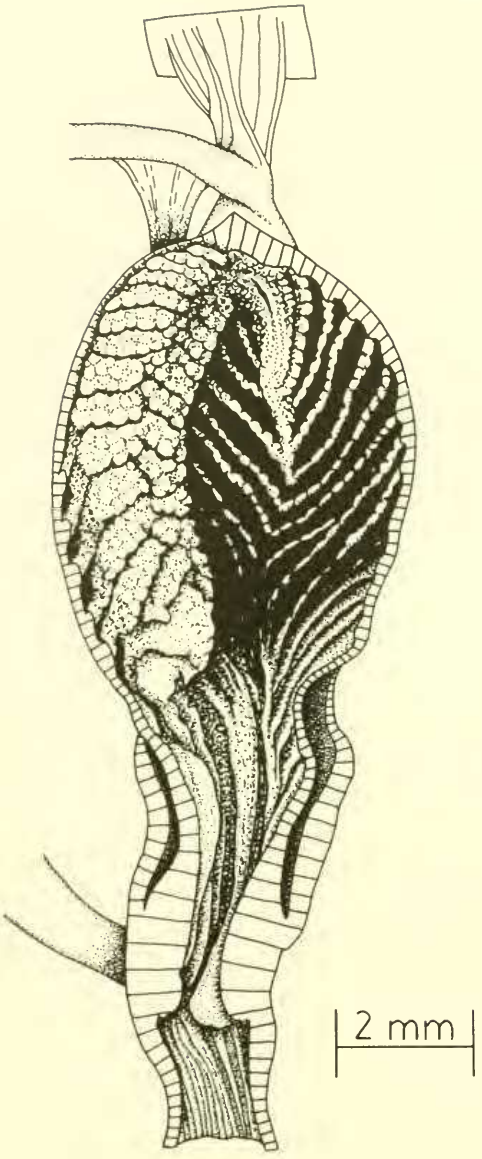

FIG. 12. Opened uneverted penial tube. *Triodopsis platysayoides* (Brooks, 1933). FMNH 214861 #1 (also dissected #2; examined Hubricht 11860 [illustrated in Solem, 1976]).

rated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing only the basal third of the penis.

Triodopsis discoidea (Pilsbry, 1904)—Dissections: 1 from 1 population. Fig. 14d. Length: 6 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, two-fifths-way from the apex in the upper, sculpted region. Verge absent. A large, smooth, fleshy peduncle present just beneath the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (2 mm) and tapered proximally (mid-width 0.5 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fourth of the penis smooth with random folds; middle fourth with slight circular corrugations; upper half sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing only the basal half of the penis.

Triodopsis fallax (Say, 1825)—Dissections: 3 from 1 population. Fig. 14b (a contracted specimen). Length: 7 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, one-fourth-way from the apex in the upper, sculpted region. Verge absent. A small, smooth, fleshy peduncle present just beneath the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (2 mm) and tapered proximally (mid-width 0.7 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fourth of the penis smooth with random folds; middle fourth with slight circular corrugations; upper half sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing only the basal half of the penis.

Triodopsis fraudulenta (Pilsbry, 1894)—Dissected 2 from 1 population. Fig. 10. Length: 6 mm. Shape like a baseball bat. Ejaculatory pore ventrally subterminal, about one-fifth-way from the penial apex in the upper, sculpted region. Verge absent. Dorsal pilaster long (3 mm) and broad (mid-width 0.8 mm), consisting of nesting horeshoe-shaped units covered with knob-like pustules about twice as large as the wall-pustules. Basal third of the penis smooth with random folds and slight circular corrugations; upper two-thirds sculpted with 15–20 columns radiating directly from the pore, the dorsal columns bearing distinct, equal-sized pustules, and the ventral columns smooth, the ventral-most merging basally into a complexly ridged protuberance. Sheath enclosing less than half of the upper, sculpted region of the penis.

Triodopsis fulciden Hubricht, 1952—Dis-

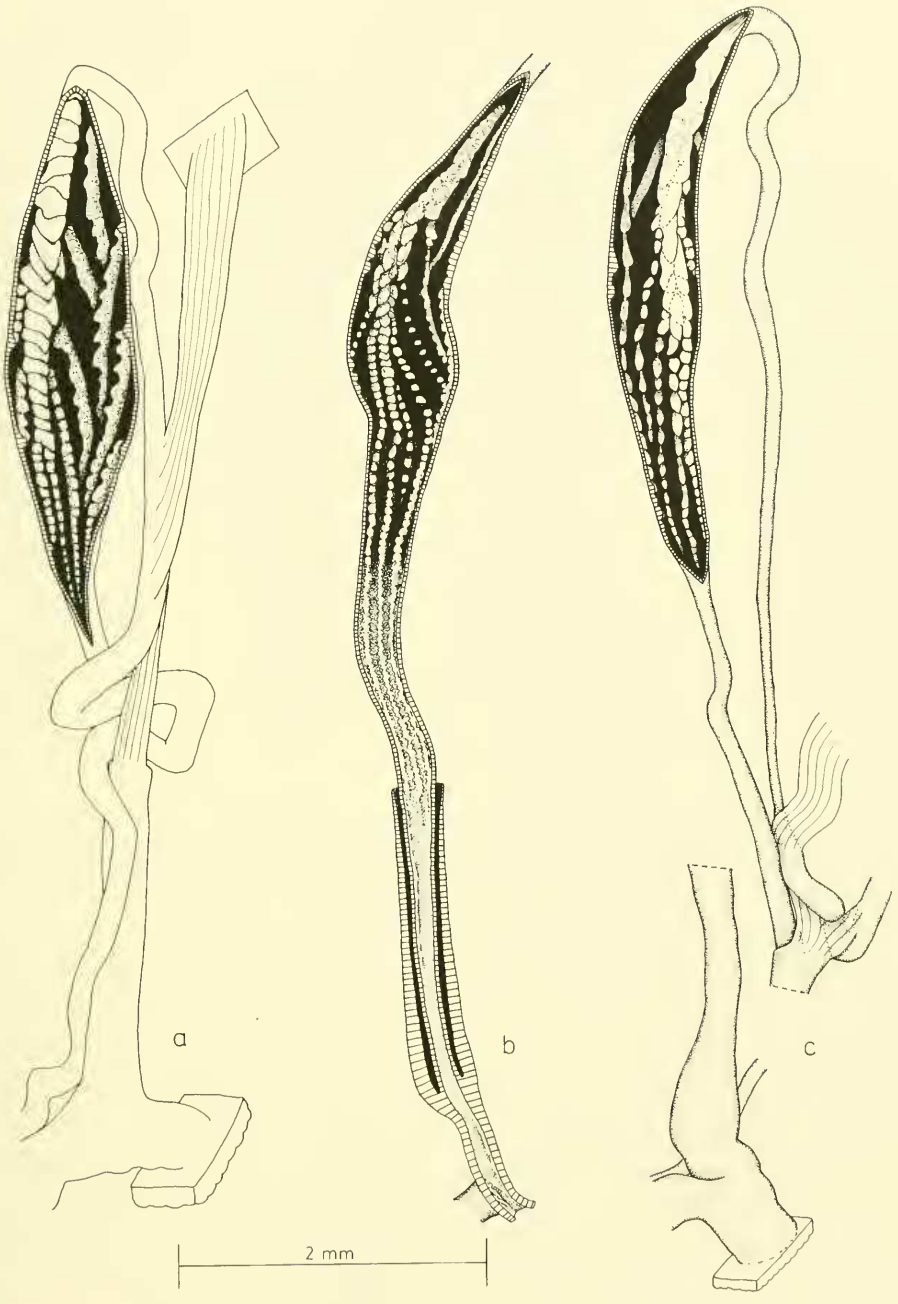

FIG. 13. Opened uneverted penial tubes. **a.** *Triodopsis vultuosa* (Gould, 1848). FMNH 214887 #A (also dissected #13: no trace of a verge; vas deferens opening terminal). **b.** *Triodopsis cragini* Call, 1886. FMNH 214803 #18 (also dissected #3: more pronounced pilaster and no sign of verge). **c.** *Triodopsis henriettae* (Mazÿck, 1877). FMNH 214824 #1: pilaster seemed partly deteriorated, with structure vague.

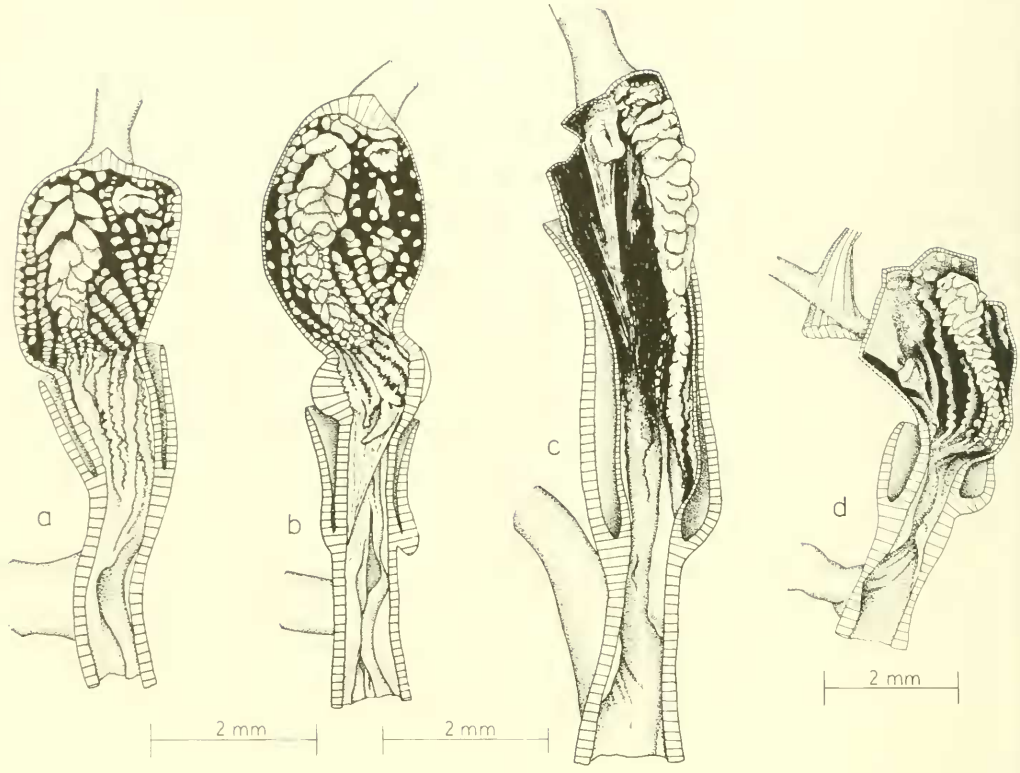

FIG 14. Opened uneverted penial tubes. **a.** *Triodopsis tridentata* (Say, 1816). FMNH 214876 (sympatric with *Triodopsis juxtidens*) #32 (also dissected 7 other populations——see Appendix C). **b.** *Triodopsis anteridon* (Pilsbry, 1940). FMNH 214796 #18 (also dissected FMNH 214793 #13, 14). **c.** *Triodopsis juxtidens* (Pilsbry, 1894). FMNH 214841 #5 (also dissected #10; FMNH 214838 #1, 2, 3; FMNH 214839 #4; FMNH 214842 #5, 6). **d.** *Triodopsis discoidea* (Pilsbry, 1904). FMNH 214811 #5.

sections: 1. Fig. 18b. Length: 3 mm. Shape like a baseball bat. Ejaculatory pore terminal. Verge absent. Dorsal pilaster two-thirds the length of the sculpted region of the penis (1 mm) and tapered proximally (mid-width 0.3 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fifth of the penis smooth with random folds: middle fifth with thick muscular walls bearing slight circular corrugations; upper three-fifths sculpted with 15–20 columns of equal-sized pustules radiating directly from the pore, the ventral columns with pustules indistinct, and the ventralmost columns merging basally. Sheath enclosing less than half of the upper, sculpted region of the penis.

Triodopsis henriettae (Mazyck, 1877)—Dissections: 2 from 1 population. Fig. 13c. Length: 9 mm. Shape like a needle. Ejaculatory pore terminal. Verge absent. Dorsal pilaster two-thirds the length of the sculpted region of the penis (2 mm) and tapered proximally (mid-width 0.2 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal third of the penis smooth with random folds; middle third with slight circular corrugations; upper third sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing only the basal third of the penis.

Triodopsis hopetonensis (Shuttleworth, 1852)—Dissections: 3 from 1 population. Fig. 15a. Length: 7 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, one-fourth-way from the apex in the upper, sculpted region. Verge absent. A small, smooth, fleshy peduncle present just beneath

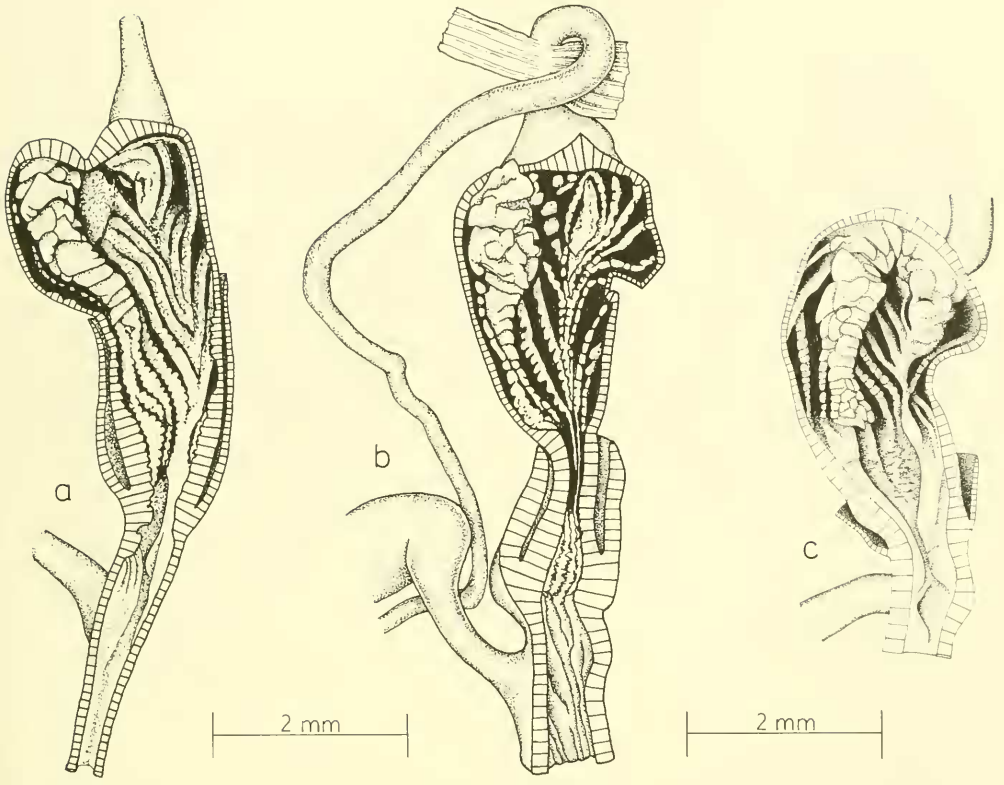

FIG. 15. Opened uneverted penial tubes. **a.** *Triodopsis hopetonensis* (Shuttleworth, 1852). FMNH 214827 #A (also dissected #15, 25). **b.** *Triodopsis palustris* Hubricht, 1958. FMNH 214857 #15 (also dissected #4, 5). **c.** *Triodopsis obsoleta* (Pilsbry, 1894). Hubricht 10300 #C (also dissected #A, B).

the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (2 mm) and tapered proximally (mid-width 0.4 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fourth of the penis smooth with random folds; middle fourth with slight circular corrugations; upper half sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing only the basal half of the penis.

Triodopsis juxtidens (Pilsbry, 1894)—Dissections: 6 from 3 populations. Fig. 14c. Length: 8 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, two-fifths-way from the apex in the upper, sculpted region. Verge absent. A large, smooth, fleshy peduncle present just beneath the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (3 mm) and tapered proximally (mid-width 0.5 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fourth of the penis smooth with random folds; middle fourth with slight circular corrugations; upper half sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing about half of the upper, sculpted region of the penis.

Triodopsis messana Hubricth, 1952—Dissections: 3 from 1 population. Fig. 16b. Length: 8 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, one-fourth-way from the apex in the upper, sculpted region. Verge absent. A small, smooth, fleshy peduncle present just beneath the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (1 mm) and tapered proximally (mid-width 0.8 mm), con-

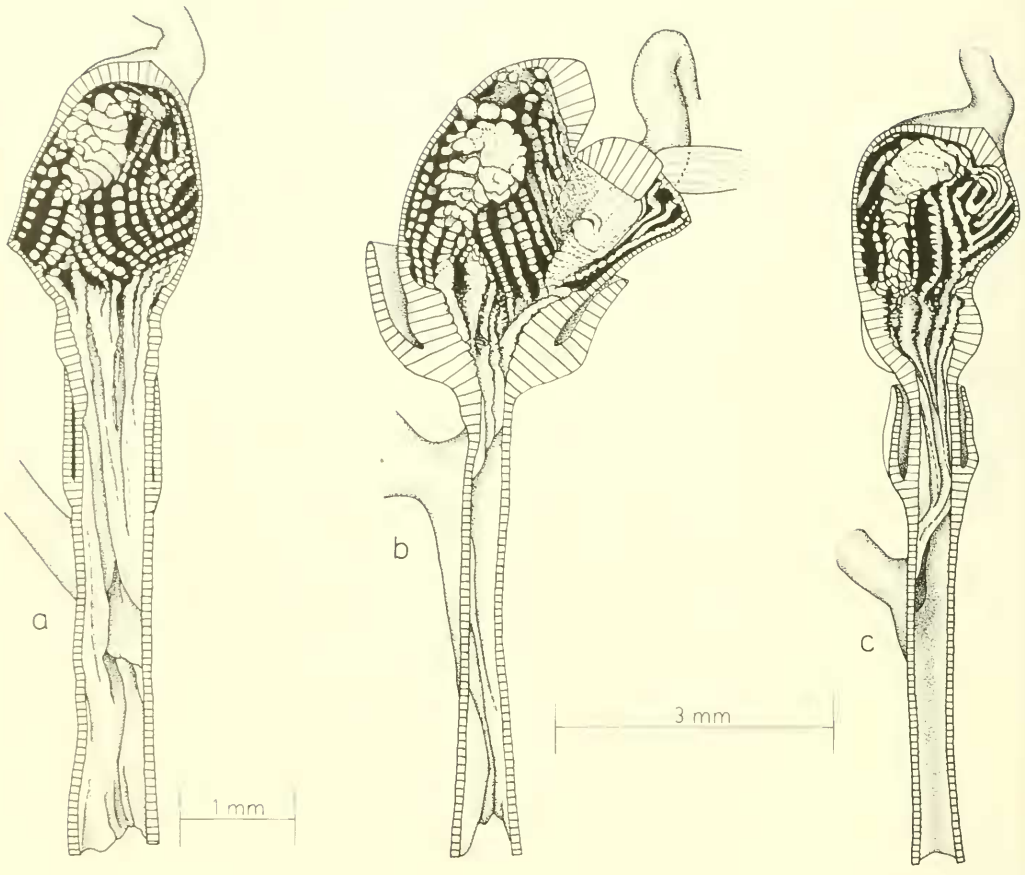

FIG. 16. Opened uneverted penial tubes. **a.** *Triodopsis alabamensis* (Pilsbry, 1902). FMNH 214791 #4 (also dissected #2: pilaster smaller and more lobular). **b.** *Triodopsis messana* Hubricht, 1952. FMNH 214846 #6 (also dissected #1 and #5, both with sculpture more effaced and with wall less tightly contracted). **c.** *Triodopsis vannostrandi* (Bland, 1875). FMNH 214880 #8 (also dissected #1 and #12, both with wall sculpture more effaced).

sisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fourth of the penis smooth with random folds; middle fourth with slight circular corrugations; upper half sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing only the basal half of the penis.

Triodopsis neglecta (Pilsbry, 1899)—Dissections: 2 from 1 population. Fig. 18a. Length: 5 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, two-fifths-way from the apex in the upper, sculpted region. Verge absent. A large, smooth, fleshy peduncle present just beneath the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (1 mm) and tapered proximally (mid-width 0.5 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fourth of the penis smooth with random folds; middle fourth with slight circular corrugations; upper half sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing less than half of the upper, sculpted region of the penis.

Triodopsis obsoleta (Pilsbry, 1894)—Dissections: 3 from 1 population. Fig. 15c (a contracted specimen). Length: 5 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, one-fourth-way from the apex in

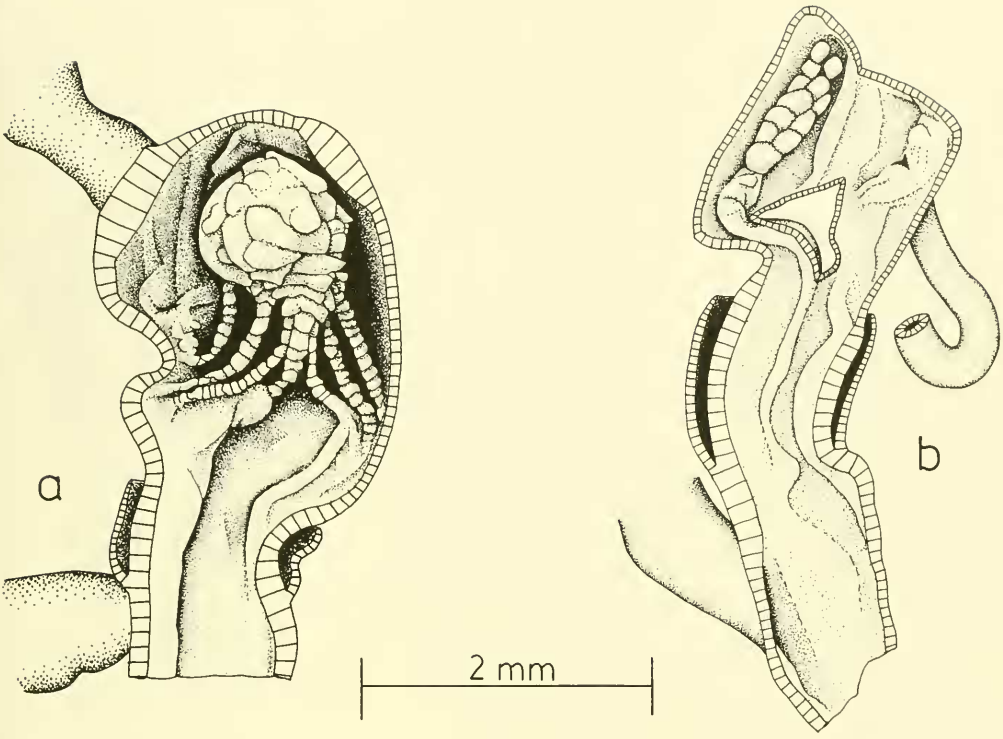

FIG. 17. Opened uneverted penial tubes. **a.** *Triodopsis fallax* (Say, 1825). Hubricht 10209 #C (also dissected #A, B). **b.** *Triodopsis soelneri* (Henderson, 1907). ANSP A2318 (alcohol-preserved soft parts pulled from shells of ANSP 93545) #B (also dissected #A, C).

the upper, sculpted region. Verge absent. A small, smooth, fleshy peduncle present just beneath the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (1 mm) and tapered proximally (mid-width 0.5 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fourth of the penis smooth with random folds; middle fourth with slight circular corrugations; upper half sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing only the basal half of the penis.

Triodopsis palustris Hubricht, 1958—Dissections: 3 from 1 population. Fig. 15b. Length: 6 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, one-fourth-way from the apex in the upper, sculpted region. Verge absent. A small, smooth, fleshy peduncle present just beneath the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (2 mm) and tapered proximally (mid-width 0.7 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fourth of the penis smooth with random folds; middle fourth with slight circular corrugations; upper half sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing only the basal half of the penis.

Triodopsis pendula Hubricht, 1952—Dissections: 1 from 1 population. Fig. 18c. Length: 5 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, two-fifths-way from the apex in the upper, sculpted region. Verge absent. A large, smooth, fleshy peduncle present just beneath the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (2 mm) and tapered proximally (mid-width 0.4 mm), consisting of abutting irregularly sized and

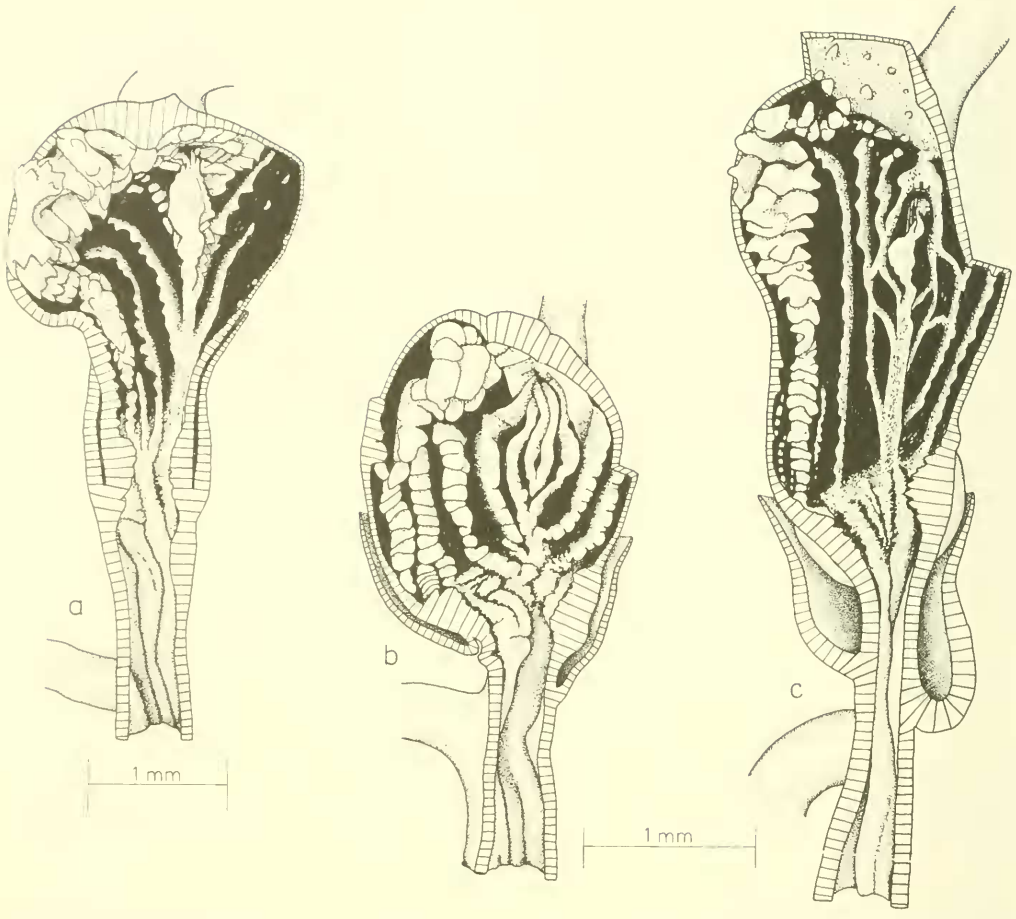

FIG. 18. Opened uneverted penial tubes. **a.** *Triodopsis neglecta* (Pilsbry, 1899). FMNH 214850 #2 (also dissected #5: no verge). **b.** *Triodopsis fulciden* Hubricht, 1952. FMNH 214823 #3. No verge; opening of vas deferens a simple hole. **c.** *Triodopsis pendula* Hubricht, 1952. FMNH 214859 #8.

shaped polygons, each bearing one to three short, blunt spurs. Basal fourth of the penis smooth with random folds; middle fourth with slight circular corrugations; upper half sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing about half of the upper, sculpted region of the penis.

Triodopsis picea Hubricht, 1958—Dissections: 2 from 1 population. Fig. 9b. Length: 10 mm. Shape like a baseball bat. Ejaculatory pore ventrally subterminal, about one-fifth-way from the penial apex in the upper, sculpted region. Verge absent. Dorsal pilaster long (3 mm) and broad (mid-width 0.9 mm), consisting of nesting horseshoe-shaped untis covered with knob-like pustules about twice as large as the wall-pustules. Basal half of the penis smooth with random folds and slight circular corrugations; upper half sculpted with 15–20 columns of distinct, equal-sized pustules radiating directly from the pore. Sheath enclosing less than half of the upper, sculpted region of the penis.

Triodopsis platysayoides (Brooks, 1933)—Dissections: 3 from 1 or 2 populations. Fig. 12. Length: 13 mm. Shape like a baseball bat. Ejaculatory pore terminal. Verge absent. Dorsal pilaster long (7 mm) and very broad (mid-width 1.7 mm), consisting of two interdigitating columns of rectangular boxes,

each covered with knob-like pustules about twice as large as the wall-pustules. Basal third of the penis smooth with random folds; upper two-thirds sculpted with equilateral, widely spaced columns of distinct, equal-sized pustules, merging ventrally into 10–12 obtuse V-shapes. Sheath enclosing less than half of the upper, sculpted region of the penis.

Triodopsis rugosa Brooks & MacMillan, 1940—Dissections: 2 from 1 population. Not illustrated but similar to Fig. 18b. Length: not measured. Shape like a baseball bat. Ejaculatory pore terminal. Verge absent. Dorsal pilaster two-thirds the length of the sculpted region of the penis and tapered proximally, consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fifth of the penis smooth with random folds; middle fifth with thick muscular walls bearing slight circular corrugations; upper three-fifths sculpted with 15–20 columns of equal-sized pustules radiating directly from the pore, the ventral columns with pustules indistinct, and the ventralmost columns merging basally. Sheath enclosing less than half of the upper, sculpted region of the penis.

Triodopsis soelneri (Henderson, 1907)—Dissections: 3 from 1 population. Fig. 17b. Length: 5 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, one-fourth-way from the apex in the upper, sculpted region. Verge absent. A small, smooth, fleshy peduncle present just beneath the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (1 mm) and tapered proximally (mid-width 0.3 mm), consisting of abutting irregularly sized and shaped polygons, each smooth and without spurs. Basal half of the penis smooth with random folds; upper half smooth with dorsal traces of equilateral, widely separated columns. Sheath enclosing only the basal half of the penis.

Triodopsis tennesseensis (Walker & Pilsbry, 1902)—Dissections: 3 from 1 population. Fig. 11b–c. Length: 6 mm. Shape like a baseball bat. Ejaculatory pore terminal. Verge absent. Dorsal pilaster short (1 mm) and broad (mid-width 0.8 mm), consisting of a solid mass bearing three tiers of long, sharp spurs. Basal third of the penis smooth with random folds and slight circular corrugations; upper two-thirds sculpted with 15–20 columns radiating directly from the pore, the dorsal columns bearing indistinct, equal-sized pustules, and the ventral columns completely smooth. Sheath enclosing less than half of the upper, sculpted region of the penis.

Triodopsis tridentata (Say, 1816)—Dissections: 10 from 8 populations. Fig. 14a. Length: 6 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, one-fourth-way from the apex in the upper, sculpted region. Verge absent. A small, smooth, fleshy peduncle present just beneath the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (2 mm) and tapered proximally (mid-width 0.7 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fourth of the penis smooth with random folds; middle fourth with slight circular corrugations; upper half sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing only the basal half of the penis.

Triodopsis vannostrandi (Bland, 1875)—Dissections: 3 from 1 population. Fig. 16c. Length: 8 mm. Shape like a mace. Ejaculatory pore ventrally subterminal, one-fourth-way from the apex in the upper, sculpted region. Verge absent. A small, smooth, fleshy peduncle present just beneath the pore. Dorsal pilaster two-thirds the length of the sculpted region of the penis (2 mm) and tapered proximally (mid-width 0.4 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal fourth of the penis smooth with random folds; middle fourth with slight circular corrugations; upper half sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing only the basal half of the penis.

Triodopsis vulgata (Pilsbry, 1940)—Dissects: 7 from 3 populations. Fig. 9a. Length: 9 mm. Shape like a baseball bat. Ejaculatory pore ventrally subterminal, about one-fifth-way from the penial apex in the upper, sculpted region. Verge absent. Dorsal pilaster long (3 mm) and broad (mid-width 0.9 mm), covered with knob-like pustules all about twice as large as the wall-pustules. Basal half of the penis smooth with random folds and slight circular corrugations; upper

half sculpted with 15–20 columns of distinct, equal-sized pustules radiating directly from the pore. Sheath enclosing less than half of the upper, sculpted region of the penis.

Triodopsis vultuosa (Gould, 1848)—Dissections: 2 from 1 population. Fig. 13a. Length: 7 mm. Shape like a needle. Ejaculatory pore terminal. Verge absent. Dorsal pilaster two-thirds the length of the sculpted region of the penis (2 mm) and tapered proximally (mid-width 0.2 mm), consisting of abutting irregularly sized and shaped polygons, each bearing one to three short, blunt spurs. Basal third of the penis smooth with random folds; middle third with slight circular corrugations; upper third sculpted with equilateral, widely separated columns of equal-sized pustules, merging ventrally into 5–7 acute V-shapes. Sheath enclosing only the basal third of the penis.

Webbhelix multilineata (Say, 1821)—Dissections: 7 from 3 populations. Fig. 6a. Length: 14 mm. Shape cylindrical, the apical half enlarged. Ejaculatory pore terminal, on a verge. Verge large (1.2 mm), terminal, dorsolaterally compressed, backpointing, with a ventrally subterminal pore, smoothly sculpted, and bearing two broad, prominent terminal papillae. Dorsal pilaster short (5 mm) and broad (mid-width 1.0 mm), proximally truncated, and covered with small, uniform, pointed pustules. Basal two-thirds of the penis smooth with random folds; upper one-third uniformly sculpted with 25–35 adjacent, generally unmerging, equilateral columns of distinct, equal-sized pustules radiating from the pore region; the pustules are indistinct on the basal two-thirds of these columns. Sheath enclosing less than half of the upper, sculpted region of the penis.

Xolotrema caroliniensis (Lea, 1834)—Dissections: 2 from 1 population. Fig. 7e. Length: 8 mm. Shaped like a pear. Ejaculatory pore ventrally subterminal, about one-third-way from the penial apex in the upper, scupted region, and on a verge. Verge small (0.2 mm), wider than long, ventrally subterminal on a slight prominence, dorso-laterally compressed, forward-pointing, with a ventrally subterminal pore and sculpted with surface cords continuing into about 4 narrow terminal papillae. Dorsal pilaster indistinct from the columns of wall pustules, and consisting of 5 broad, nested A-shapes. Basal one-third of the penis smooth with random folds; upper two-thirds sculpted with slightly separated columns of cuboidal, rough-surfaced pustules, enlarging and merging and ventrally into 6–10 tapered U-shapes. Sheath enclosing less than half of the upper, sculpted region of the penis.

Xolotrema denotata (Férussac, 1821)—Dissections: 3 from 1 population. Fig. 7a–b. Length: 9 mm. Shaped like a pear. Ejaculatory pore ventrally subterminal, about one-third-way from the penial apex in the upper, scupted region, and on a verge. Verge small (0.2 mm), wider than long, ventrally subterminal on a slight prominence, dorso-laterally compressed, forward-pointing, with a ventrally subterminal pore and sculpted with surface cords continuing into about 4 narrow terminal papillae (Fig. 7b). Dorsal pilaster indistinct from the columns of wall pustules, and consisting of 5 broad, nested A-shapes. Basal one-third of the penis smooth with random folds; upper two-thirds sculpted with slightly separated columns of cuboidal, rough-surfaced pustules, enlarging and merging and ventrally into 6–10 tapered U-shapes. Sheath enclosing less than half of the upper, sculpted region of the penis.

Xolotrema fosteri (F. C. Baker, 1932)—Dissections: 6 from 2 populations. Fig. 8a. Length: 8 mm. Shape cylindrical. Ejaculatory pore terminal, on a verge. Verge small (0.2 mm), longer than wide, terminal, dorso-laterally compressed, backpointing, with a ventrally subterminal pore and sculpted with surface cords continuing into about 6 terminal papillae. Dorsal pilaster short (2 mm), moderately wide (mid-width 0.3 mm), and superficially resembling a single column of abutting cubes. Ventral surface bearing a long, smooth-surfaced, fleshy column with a central, longitudinal, shallow groove. Basal third of the penis smooth with random folds; middle third slightly bulbous and corrugated by bands of circular and longitudinal muscles; upper third sculpted with slightly separated columns of cuboidal, smooth-surfaced pustules, enlarging and merging and ventrally into 6–10 tapered U-shapes. Sheath enclosing the entire upper, sculpted region of the penis.

Xolotrema obstricta (Say, 1821)—Dissections: 2 from 1 population. Fig. 7c–d. Length: 11 mm. Shaped like an inverted pear.

Ejaculatory pore ventrally subterminal, about one-third-way from the penial apex in the upper, sculpted region, and on a verge. Verge small (0.2 mm), wider than long, ventrally subterminal on a slight prominence, dorsolaterally compressed, forward-pointing, with a ventrally subterminal pore and sculpted with surface cords continuing into about 4 narrow terminal papillae (Fig. 7d). Dorsal pilaster indistinct from the columns of wall pustules, and consisting of 5 broad, nested A-shapes. Basal one-third of the penis smooth with random folds; upper two-thirds sculpted with slightly separated columns of cuboidal, rough-surfaced pustules, enlarging and merging and ventrally into 6–10 tapered U-shapes. Sheath enclosing less than half of the upper, sculpted region of the penis.

Xolotrema occidentalis (Pilsbry & Ferriss, 1907)—Dissections: 1 from 1 population. Fig. 8b–c. Length: 7 mm. Shape cylindrical (in Fig. 8b, it appears clubbed because of contraction within the sheath). Ejaculatory pore terminal, on a verge. Verge small (0.3 mm), longer than wide, terminal, dorsolaterally compressed, back-pointing, with a ventrally subterminal pore and sculpted with surface cords continuing into about 6 terminal papillae (Fig. 8c). Dorsal pilaster short (1 mm), moderately wide (mid-width 0.3 mm), and superficially resembling a single column of abutting cubes. Ventral surface bearing a long, smooth-surfaced, fleshy column with a central, longitudinal, shallow groove (this structure is contracted and distorted in Fig. 8b). Basal third of the penis smooth with random folds; middle third slightly bulbous and corrugated by bands of circular and longitudinal muscles; upper third sculpted with slightly separated columns of cuboidal, smooth-surfaced pustules, enlarging and merging and ventrally into 6–10 tapered U-shapes. Sheath enclosing the entire upper, sculpted region of the penis.

Suggested character-state transformations

The total variation in penial morphology was classified into 10 characters comprising 60 character states. These are arranged into their suggested phylogenies in Figs. 19–23, in which the suggested character-state transformations are numbered 1–50.

The dorsal pilaster (Character 1) was the most variable penial-morphological character. Twenty-two states (including its absence in the outgroups) were detected, none of which appeared to be convergent. Their suggested phylogeny (Fig. 19) contains transformations 1–21.

Pustules on the penial wall (Character 2) yielded 11 character-states, with two sets of convergences, each involving three character-states: types 1, 2, and 3 chevrons; and 3 types of smooth columns (explained below). The suggested phylogeny (Fig. 20) involves transformations 22–33.

Verges (Character 3) occur in several of the outgroups of eastern triodopsines: *Vespericola,* Oreohelicidae, and some Camaenidae. These verges, because of their structural differences (discussed below), presumably are convergent on, rather than plesiomorphous with, the eastern-triodopsine verge. Six character states were detected, three of which appeared convergent (types 1, 2, and 3 small verges). The suggested character-state phylogeny (Fig. 21) embodies transformations 34-38.

The position on the penis of the ejaculatory pore, or opening of the vas deferens (Character 4), varied as 6 distinct character states, 4 of which appeared convergent (dorsally subterminal, and types 1, 2, and 3 ventrally subterminal). Evolution of a ventrally subterminal pore is probably easily achieved developmentally by overgrowth of the dorsal penial wall. This presumably is functionally adaptive because it both plugs the mate's spermathecal duct during copulation (with the overgrown apical knob of the penis) and emits the sperm mass beneath the plug and away from the digestive spermathecal bursa (Emberton, 1986). The convergences were detected by differences in penial shape and in details of pore position and structure, as explained below. The suggested character-state phylogeny (Fig. 22) contains transformations 39–43.

Characters 5–10 (ventral pilaster, basal penis length, ventral sperm channel, sheath length, upper penis length, and peduncle) each had two or three character states, suggested to be linked by one or two transformations (Fig. 23, transformations 44–50).

In presenting each of the 50 suggested character-state transformations below, the same format has been used throughout: (1) the transformation's identification number as used in Figs. 19–23; (2) the identification numbers of the transformation or series of transformations suggested to have preceded it evolutionarily; (3) the suggested plesio-

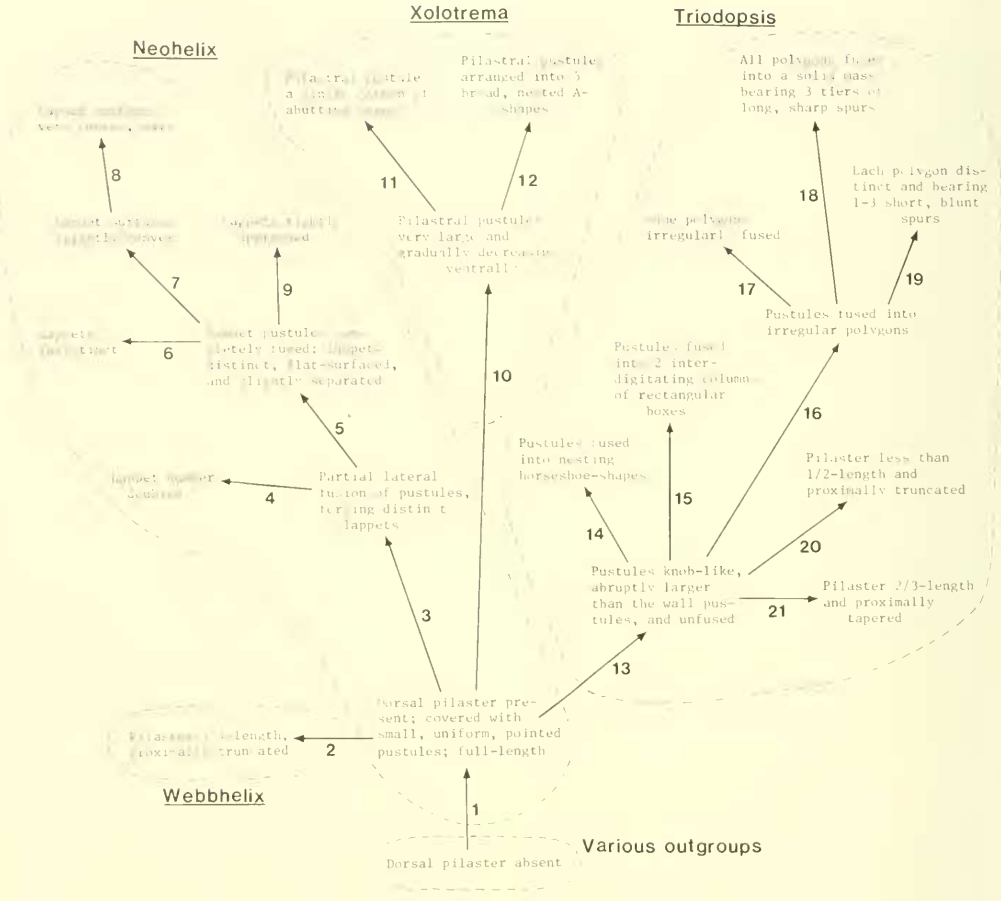

FIG. 19. Suggested character-state transformations in eastern American triodopsine penial morphology. Character 1, pilaster and pilastral pustules.

morphous state; (4) the outgroup taxa possessing the suggested plesiomorphous state; (5) the suggested apomorphous state; (6) the taxa suggested to have formerly possessed the apomorphous state, *although lacking it now;* (7) the taxa which now possess the suggested apomorphous state; and (8) a discussion of the suggested transformation, including its further explanation, if necessary, and its justification.

Transformation 1—Preceding transformations: none.

Plesiomorphous state: dorsal pilaster absent. Present in: *Cryptomastix, Allogona, Ashmunella, Oreohelix, Polygyrella,* Polygyracea, and the camaenids *Amplirhagada* and *Torresitrachea.*

Apomorphous state: dorsal pilaster present, covered with unmodified pustules, and full-length. Formerly present in: all eastern triodopsines (Figs. 2–18). Now present in: *Webbhelix multilineata* (Fig. 6a).

Discussion. Emberton (1986) discussed the evidence that this type of single dorsal pilaster, formed by a longitudinal outgrowth from the penial wall, is unique to triodopsines within the Polygyridae and their outgroups (a similar pilaster in some Australian camaenids is considered convergent). It apparently occurs in all eastern triodopsines (Figs. 2–18); although it is not at all obvious in the dissections of *Xolotrema* (Figs. 7, 8), it shows up clearly in cross-sections of the penes of *X. denotata* and *X. fosteri* (Pilsbry 1940, fig. 473 #6b, 7b: 793), so presumably occurs

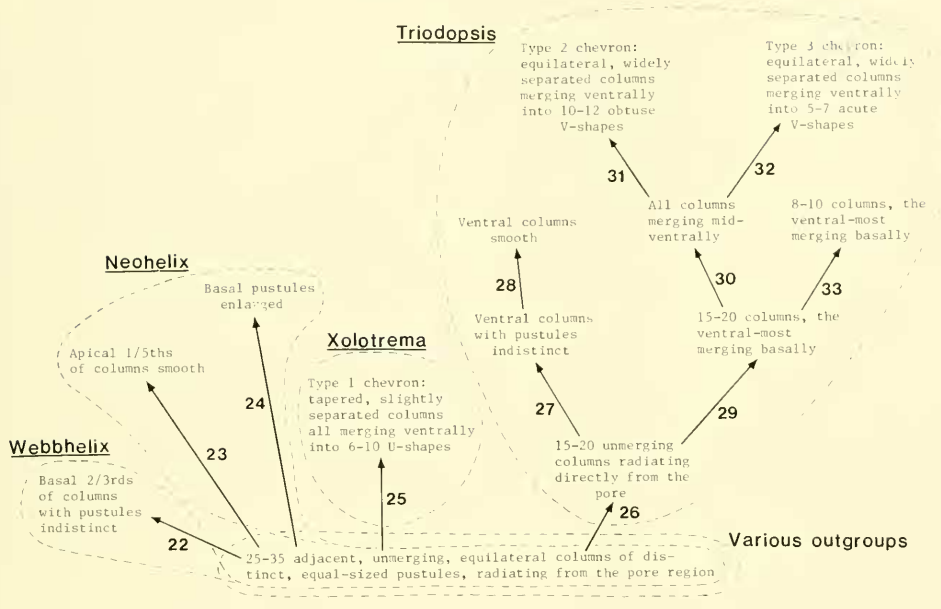

FIG. 20. Suggested character-state transformations in eastern American triodopsine penial morphology. Character 2, wall pustules.

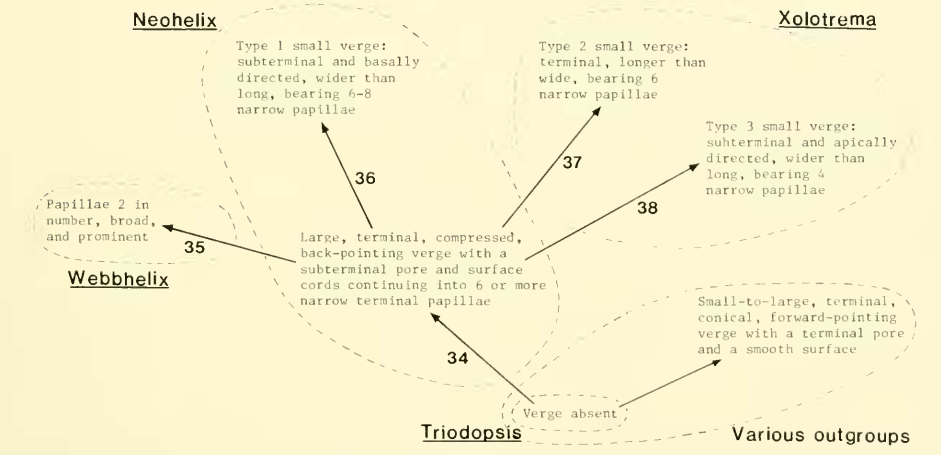

FIG. 21. Suggested character-state transformations in eastern American triodopsine penial morphology. Character 3, verge.

throughout the genus. It is assumed, for want of evidence to the contrary and because a similar structure appears nowhere else among the Polygyridae or their outgroups, that this single dorsal pilaster arose only once, so is homologous throughout eastern triodopsines. Its great variation in gross appearance appears to be attributable to differences in the patterns of fusion and enlargement of the pilastral pustules.

The most plesiomorphous pilastral sculpture appears to be that seen in *Webbhelix multilineata* (Fig. 6a). This pilastral sculpture is identical with the plesiomorphous wall

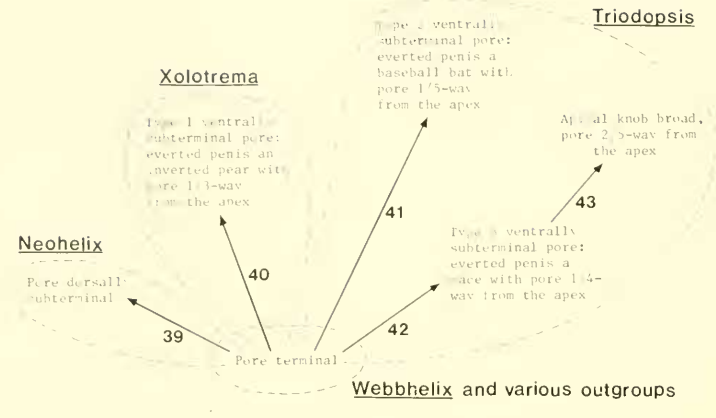

FIG. 22. Suggested character-state transformations in eastern American triodopsine penial morphology. Character 4, pore position.

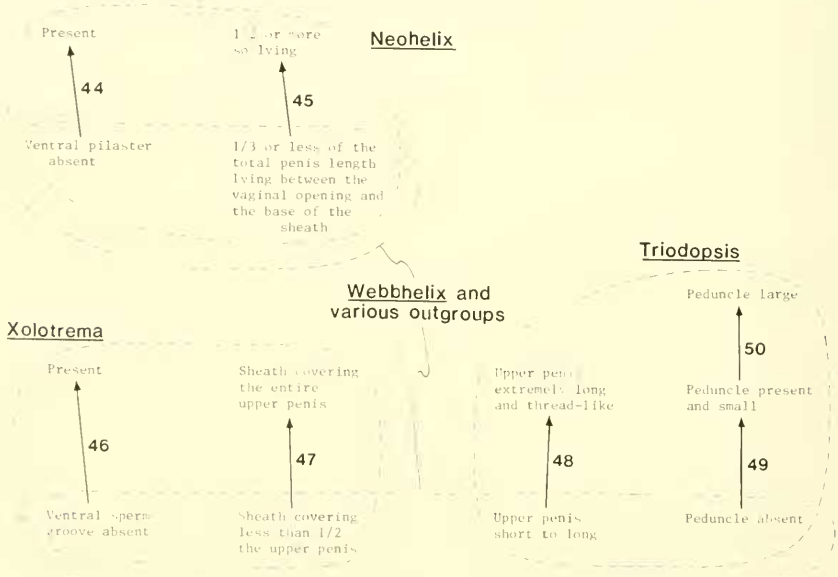

FIG. 23. Suggested character-state transformations in eastern American triodopsine penial morphology. Characters 5–10, ventral pilaster, basal penis length, ventral sperm groove, sheath length, upper penis length, and peduncle.

sculpture: adjacent, longitudinal columns of equal-sized pustules.

Transformation 2—Preceding transformations: 1.

Plesiomorphous state: pilaster full-length. Present in (outgroups): *Neohelix* (Figs. 2–5, 6b); *Xolotrema* (Figs. 7, 8); and *Triodopsis vulgata, picea, claibornensis* (Fig. 9), *burchi* (Fig. 11a), and *platysayoides* (Fig. 12).

Apomorphous state: pilaster 3/4-length and proximally truncated. Formerly and now present in: *Webbhelix multilineata* (Fig. 6a).

Discussion: This character state is unique to *W. multilineata,* so presumably is apomorphous.

Transformation 3—Preceding transformations: 1.

Plesiomorphous state: pilaster covered with unmodified pustules. Present in (outgroup): *Webbhelix multilineata* (Fig. 6a).

Apomorphous state: pilastral pustules partially fused laterally to form lappets. Formerly present in: all *Neohelix* (Figs. 2–5, 6b). Now present in: *Neohelix dentifera* (Fig. 2a, b), *lioderma* (Fig. 5a, c), and *divesta* (Fig. 5d, f).

Discussion. There appears to be a continuum from the totally unfused pilastral pustules of *W. multilineata* (Fig. 6a), to the laterally appressed slightly fused pilastral pustules of *N. dentifera* (Fig. 2b), to the partially laterally fused pilastral pustules of *N. lioderma* (Fig. 5c) and *N. divesta* (Fig. 5f), and the assumption is that this represents a true transformation series. This lateral fusion of pilastral pustules results in a column of overlapping, plate-like elements called "lappets" (Figs. 1, 2a, 5a, d).

Transformation 4—Preceding transformations: 1, 3.

Plesiomorphous state: lappets approximately equal in number to the number of columns of wall pustules. Present in (outgroup): *Neohelix albolabris* (Fig. 2d), *alleni* (Fig. 3a, c), *major* (Fig. 4a), and *solemi* (Fig. 6b).

Apomorphous state: lappet number doubled. Formerly and now present in: *Neohelix dentifera* (Fig. 2a), *lioderma* (Fig. 5a), and *divesta* (Fig. 5d).

Discussion. There are two distinct types of lappetted dorsal pilaster. In the first type, the number of pilastral lappets is approximately equal to (or somewhat greater than) the number of columns of wall pustules, as seen in *albolabris, alleni, major,* and *solemi.* In the other type, the number of pilastral lappets is approximately equal to twice the number of columns of wall pustules, as seen in *dentifera, lioderma,* and *divesta.* There are no intermediates between these two types. It appears likely that the double-lappet sculpture is derived from the single-lappet sculpture, possibly via a simple, one-step modification in a developmental program.

Transformation 5—Preceding transformations: 1, 3.

Plesiomorphous state: lappet pustules partially fused. Present in (outgroups): *Neohelix dentifera* (Figs. 2a, b), *lioderma* (Fig. 5a, c), and *divesta* (Fig. 5d, f).

Apomorphous state: lappet pustules completely fused. Formerly and now present in: *Neohelix albolabris* (Fig. 2d, e), *alleni* (Fig. 3a, c), *major* (Fig. 4a), and *solemi* (Fig. 6b).

Discussion. Although the lappets of *alleni,* and *major,* and *solemi* appear to have lost all trace of the pustules from which they presumably originated by lateral fusion, those of *albolabris* and *solemi* show a regular pattern of indentations (Figs. 2e and 6b) which seem to correspond to pustules (compare with Fig. 5c, f).

Transformation 6—Preceding transformations: 1, 3, 5.

Plesiomorphous state: lappets distinct. Present in (outgroups): *Neohelix dentifera, albolabris, alleni, major, lioderma,* and *divesta* (Figs. 2–5).

Apomorphous state: lappets indistinct. Formerly and now present in: *Neohelix solemi* (Fig. 6b).

Discussion: The dorsal pilaster of *solemi,* which appears on the right in Fig. 6b and is not to be confused with the ventral pilaster (unique to *solemi*) which appears in the center in Fig. 6b, is reduced in size and length due to the uniquely dorsally subterminal pore position (Transformation 38). Its lappets are indistinct and unequal in size, and may be vestigial now that a ventral pilaster is present.

Transformation 7—Preceding transformations: 1, 3, 5.

Plesiomorphous state: lappets flat-surfaced. Present in (outgroups): *Neohelix dentifera* (Fig. 2a), *alleni* (Fig. 3c), *lioderma* (Fig. 5a), and *divesta* (Fig. 5d).

Apomorphous state: lappets slightly convexly surfaced. Formerly present in: *albolabris* (Fig. 2d, e) and *major* (Fig. 4a). Now present in: *albolabris* (Fig. 2d, e).

Discussion. The convexity of *albolabris's* pilastral lappets (Fig. 2e) seems to result from a trend toward enlargement of the lappets which is continued in Transformation 8.

Transformation 8—Preceding transformations: 1, 3, 5, 7.

Plesiomorphous state: lappets slightly convexly surfaced. Present in (outgroup): *Neohelix albolabris* (Fig. 2d, e).

Apomorphous state: lappet surfaces very convex and irregularly wavy. Formerly and now present in: *Neohelix major* (Fig. 4a).

Discussion. This character state is unique

to *major*, which has the largest pilastral lappets, so presumably is apomorphous.

Transformation 9—Preceding transformations: 1, 3, 5.

Plesiomorphous state: lappets slightly separated. Present in (outgroups): *Neohelix albolabris* (Fig. 2a, e), *major* (Fig. 4a), and *solemi* (Fig. 6b).

Apomorphous state: lappets tightly appressed. Formerly and now present in: *Neohelix alleni* (Fig. 3c).

Discussion: The lappets are extremely smooth-surfaced and fit tightly together so that the general pilastral surface is relatively flat (Fig. 3c). Fig. 3a was accidently incorrectly shaded and does not properly represent this character state.

Transformation 10—Preceding transformations: 1.

Plesiomorphous state: pilastral pustules small and uniform in size. Present in (outgroup): *Webbhelix multilineata* (Fig. 6a).

Apomorphous state: pilastral pustules very large and gradually decreasing in size ventrally. Formerly and now present in: *Xolotrema* (Figs. 7a, c, e; 8a, b).

Discussion. *Xolotrema's* dorsal pilaster is unique and quite disjunct from any other found in eastern triodopsines. Its derivation from the *W. multilineata*-type is a best guess which is supported by the homologous verge (Character 3) between *Webbhelix* and *Xolotrema*. Whether the large pilastral pustules originated by enlargement, or fusion, or both, is beyond conjecture at this point.

Transformation 11—Preceding transformations: 1, 10.

Plesiomorphous state: pilastral pustules very large and gradually decreasing in size ventrally, but of unknown mid-dorsal configuration. Formerly present in: hypothesized common ancestor of *Xolotrema denotata, obstricta, caroliniensis, fosteri,* and *occidentalis* (Figs. 7, 8). Now present in: none.

Apomorphous state: pilastral pustules a single column of abutting cubes. Formerly and now present in: *Xolotrema fosteri* (Fig. 8a) and *occidentalis* (Fig. 8b).

Discussion. The superficial resemblance of *fosteri's* and *occidentalis's* pilastral elements (Fig. 8a, b) to lappets (e.g., Figs. 2d, 3a) and to polygons (e.g. Figs. 14a, 15a) breaks down on close examination; these three types appear to be nonhomologous. The dorsal pilaster of *fosteri* and *occidentalis* should not be confused with the ventral sperm groove (Figs. 8a, b) which occurs in these two species.

Transformation 12—Preceding transformations: 1, 10.

Plesiomorphous state: pilastral pustules very large and gradually decreasing in size ventrally, but of unknown mid-dorsal configuration. Present in: hypothesized common ancestor of *Xolotrema denotata, obstricta, caroliniensis, fosteri,* and *occidentalis* (Figs. 7, 8).

Apomorphous state: pilastral pustules arranged into 5 broad, nested A-shapes. Formerly and now present in: *Xolotrema denotata* (Fig. 7a), *obstricta* (Fig. 7c), and *caroliniensis* (Fig. 7e).

Discussion. The dorsal pilaster in *denotata, obstricta,* and *caroliniensis* is less obvious than in any other eastern triodopsines. The thickening of the dorsal penial wall which forms the dorsal pilaster is reduced in these species (Pilsbry 1940, fig. 473 #6b) to the extent that it is not at all evident in Fig. 7a, c, e. The swollen area beneath the subterminal verge in these species is easily mistaken for the dorsal pilaster, but the fact that the verge points up indicates that this is actually the ventral side of the penis, so the dorsal pilaster is on the opposite side (Fig. 7a, c, e), which is heavily sculpted with A-shaped arrangements of broad, rugose pustules. The substructural complexity of these pustules suggests that they resulted from fusion of smaller, plesiomorphous pustules. Despite the great difference between the dorsal pilastral sculptures of *denotata, obstricta,* and *caroliniensis* on one the hand (Fig. 7), and *fosteri* and *occidentalis* on the other hand (Fig. 8), their similarity in the broad, flat-surfaced, ventrally-diminishing pilastral pustules, as well as their apparent homologies in wall pustules (Character 2) and verge (Character 3), lead to the suggestion that their dorsal pilasters arose from a common, unknown ancestral type.

Transformation 13—Preceding transformation: 1.

Plesiomorphous state: pilastral pustules pointed and uniformly equal in size to the wall pustules. Present in (outgroup): *Webbhelix multilineata* (Fig. 6a).

Apomorphous state: pilastral pustules knob-like and abruptly larger than the wall pustules. Formerly present in: all *Triodopsis*

(Figs. 9–18). Now present in: *T. vulgata* (Fig. 9a) and *T. claibornensis* (Fig. 9c).

Discussion. Knob-like pilastral pustules about twice as large as the wall pustules, with no ventral intergradation in size, occur either unfused or fused in various ways in *vulgata, picea, claibornensis* (Fig. 9), *burchi* (Fig. 11a), and *platysayoides* (Fig. 12). The most similar pilastral sculpture, and one from which this type could easily have evolved, is that of *W. multilineata* (Fig. 6a), in which the pilastral pustules are more pointed and scale-like, and equal in size to the wall pustules: simple enlargement would have sufficed.

Transformation 14—Preceding transformations: 1, 13.

Plesiomorphous state: knob-like pilastral pustules unfused. Present in (outgroup): *Triodopsis vulgata* (Fig. 9a) and *claibornensis* (Fig. 9c).

Apomorphous state: pilaster sculpted with nesting horseshoe-shaped elements with a knobby surface. Formerly and now present in: *Triodopsis picea* (Fig. 9b).

Discussion. Despite their apparent fusion into this pattern, the apical knobs of the pilastral pustules are readily apparent in *picea*.

Transformation 15—Preceding transformations: 1, 13.

Plesiomorphous state: knob-like pilastral pustules unfused. Present in (outgroup): *Triodopsis vulgata* (Fig. 9a) and *claibornensis* (Fig. 9c).

Apomorphous state: pilaster sculpted with rectangular box-like elements with knobby surfaces and arranged in two interdigitating columns. Formerly and now present in *Triodopsis platysayoides* (Fig. 12).

Discussion. The knobby surface of *playtsayoides's* pilaster suggests that its box-like elements derived by fusion from the knob-like pilastral pustules seen in *vulgata* and *claibornensis*.

Transformation 16—Preceding transformations: 1, 13.

Plesiomorphous state: knob-like pilastral pustules unfused. Present in (outgroup): *Triodopsis vulgata* (Fig. 9a) and *claibornensis* (Fig. 9c).

Apomorphous state: pilaster sculpted with elements (polygons) 4–10 times the size of wall pustules and bearing 2–5 knobs. Formerly present in: hypothesized ancestor of all of *Triodopsis* except *vulgata, picea, claibornensis,* and *platysayoides* (Figs. 10, 11, 13–18). Now present in: none.

Discussion. These polygonal pilastral elements, which occur with modification throughout most of *Triodopsis,* have a surface sculpture or substructure reminiscent of the unfused pilastral pustules of *vulgata* and *claibornensis* (Fig. 9a, c)—this is especially evident in the illustration of *messana* (Fig. 16b)—so the assumption is that they were derived from these by fusion.

Transformation 17—Preceding transformations: 1, 13, 16?

Plesiomorphous state (?): knobby-surfaced pilastral polygons. Present in (outgroup): hypothesized ancestor approximated by the illustration of *Triodopsis messana* (Fig. 16b).

Apomorphous state: knobby-surfaced pilastral elements 1–2 times as large as polygons. Formerly and now present in: *Triodopsis burchi* (Fig. 11a).

Discussion. The pilastral sculpture of *burchi* is unique and problematic. Because of its knobby surface, it probably derived from either a *vulgata*-type ancestor (Fig. 9a) or a hypothesized ancestor in which partial fusion (into polygons) of the pilastral pustules had already taken place. The latter alternative was chosen because the irregular size and pattern of *burchi's* pilastral elements suggest that intermediate fusion has taken taken place.

Transformation 18—Preceding transformations: 1, 13, 16?

Plesiomorphous state (?): knobby-surfaced pilastral polygons. Present in (outgroup): hypothesized ancestor approximated by the illustration of *Triodopsis messana* (Fig. 16b).

Apomorphous state: dorsal pilaster a solid, rounded mass bearing about 3 tiers of long, sharp spurs. Formerly and now present in: *Triodopsis tennesseensis* (Fig. 11b) and *complanata* (Fig. 11d).

Discussion. This is another unique and problematic form of the dorsal pilaster. The spurs are so much longer, sharper, and more regularly arranged than are the blunt spurs of Transformation 19 that they are probably not homologous. The substructure of *complanata's* pilaster (Fig. 11d) somewhat resembles a hypertrophied and regularized form of, for example, the pilaster of *tridentata* (Fig. 14a), so it may have derived from a pilaster with polygonal elements.

Transformation 19—Preceding transformations: 1, 13, 16.

Plesiomorphous state: pilastral polygons with simple knobby surface. Present in (outgroup): hypothesized ancestor most closely approximated by the illustration of *Triodopsis messana* (Fig. 16b).

Apomorphous state: pilastral polygons bearing blunt spurs. Formerly and now present in: *Triodopsis fraudulenta* (Fig. 10), *vultuosa, cragini, henriettae, tridentata, anteridon, juxtidens, discoidea, hopetonensis, palustris, obsoleta, alabamensis, messana, vannostrandi* (Figs. 13–16); *fallax* (Fig. 17a), *neglecta, fulciden,* and *pendula* (Fig. 18).

Discussion. The blunt spurs, which are most obvious in the illustrations of *vultuosa* (Fig. 13a), *tridentata* (Fig. 14a), *anteridon* (Fig. 14b), and *alabamensis* (Fig. 16a), appear to be derived by outgrowth of the individual pustules which originally fused (Transformation 16) to form the polygons.

Transformation 20—Preceding transformations: 1.

Plesiomorphous state: dorsal pilaster full-length. Present in (outgroups): *Webbhelix* (Fig. 6a), *Neohelix* (Figs. 2–5, 6b);*Xolotrema* (Figs. 7, 8); and *Triodopsis vulgata, picea, claibornensis* (Fig. 9), *burchi* (Fig. 11a), and *platysayoides* (Fig. 12).

Apomorphous state: dorsal pilaster less than 1/2 length and proximally truncated. Formerly and now present in: *Triodopsis tennesseensis* (Fig. 11b) and *complanata* (Fig. 11d).

Discussion. This short pilaster appears apomorphous relative to the taxonomically widespread and probably ontogenetically more easily achieveable full-length pilaster.

Transformation 21—Preceding transformations: 1.

Plesiomorphous state: dorsal pilaster full-length. Present in (outgroups): *Webbhelix* (Fig. 6a), *Neohelix* (Figs. 2–5, 6b); *Xolotrema* (Figs. 7, 8); and *Triodopsis vulgata, picea, claibornensis* (Fig. 9), *burchi* (Fig. 11a), and *platysayoides* (Fig. 12).

Apomorphous state: dorsal pilaster 2/3 length and proximally tapered. Formerly and now present in: *Triodopsis fraudulenta* (Fig. 10), *vultuosa, cragini, henriettae, tridentata, anteridon, juxtidens, discoidea, hopetonensis, palustris, obsoleta, alabamensis, messana, vannostrandi* (Figs. 13–16), *fallax* (Fig. 17a), *neglecta, fulciden,* and *pendula* (Fig. 18).

Discussion. For the same reasons cited for Transformation 20, it is assumed that this shortened pilaster is apomorphous.

Transformation 22—Preceding transformations: none.

Plesiomorphous state: all wall columns bearing distinct pustules along their entire lengths. Present in (outgroups): some Camaenidae, Oreohelicidae, and Ashmunellinae; all *Neohelix* except *alleni* (Figs. 2, 4, 5, 6b).

Apomorphous state: all wall columns with pustules indistinct basally. Formerly and now present in: *Webbhelix multilineata* (Fig. 6a).

Discussion. Despite their partial fusion in *multilineata,* the wall pustules are still evident and give the penial wall a rough surface sculpture. Thus this character state differs from the smooth pustular columns discussed under Transformations 23, 27, and 28.

Transformation 23—Preceding transformations: none.

Plesiomorphous state: all wall columns bearing distinct pustules along their entire lengths. Present in (outgroups): some Camaenidae, Oreohelicidae, and Ashmunellinae; all *Neohelix* except *alleni* (Figs. 2, 3, 5, 6b).

Apomorphous state: all wall columns with their apical 1/5th to 1/4th smooth, with no trace of pustules. Formerly and now present in: *N. alleni* (Fig. 3).

Discussion. Although smooth wall columns occur in some other eastern triodopsines (Transformations 27 and 28), the apical localization seen in *alleni* is unique and surely nonhomologous.

Transformation 24—Preceding transformations: none.

Plesiomorphous state: all wall pustules approximately equal in size or smaller basally. Present in (outgroups): some Camaenidae, Oreohelicidae, and Ashmunellinae; all *Neohelix* except *dentifera, lioderma,* and *divesta* (Figs. 2d, 3, 4, 6).

Apomorphous state: basal wall pustules more than twice as large as the apical wall pustules. Formerly and now present in: *Neohelix dentifera* (Fig. 2a), *lioderma* (Fig. 5a), and *divesta* (Fig. 5d).

Discussion. There is variation within the apomorphous state: in *dentifera* the basal enlargement is more localized and abrupt than in *lioderma* and *divesta.* Because it is

unclear which of these variations would be plesiomorphous to the other, they were left together as one apparently homologous, apomorphous state.

Transformation 25—Preceding transformations: none.

Plesiomorphous state: wall columns unmerging, 25–35 in number, linear, equilateral, adjacent, and bearing equal sized-pustules. Present in (outgroups): some Camaenidae, Oreohelicidae, and Ashmunellinae; *Webbhelix;* all *Neohelix* except *dentifera, lioderma,* and *divesta* (Figs. 2d, 3, 4, 6).

Apomorphous state: Type 1 chevron: wall columns all merging mid-ventrally into 6–10 U-shapes, tapered, slightly separated, and bearing unequally sized pustules. Formerly and now present in: *Xolotrema* (Figs. 7, 8).

Discussion. This and similar patterns are being called "chevrons" because the ventral wall resembles an inverted chevron. Despite a superficial similarity to Types 2 and 3 chevrons (Transformations 31 and 32), the Type 1 chevron can be recognized as convergent by its ventral U- rather than V-shapes, its tapered rather than equilateral columns, its slightly rather than widely separated columns, its unequally rather than equally sized pustules, and its flat-surfaced rather than pointed pustules. The gap between the Type 1 chevron and its hypothesized plesiomorphous state is great and there are no other character states that appear transitional. The series represented by Transformations 29, 30, and 31 or 32 (discussed below) outlines a possible path similar to one by which the Type 1 chevron may have arisen independently.

Transformation 26—Preceding transformations: none.

Plesiomorphous state: 25–35 columns radiating from the pore region and adjacent and equally sized along their entire lengths. Present in (outgroups): some Camaenidae, Oreohelicidae, and Ashmunellinae; *Webbhelix;* and *Neohelix* (Figs. 2–6).

Apomorphous state: 15–20 columns radiating directly from and diverging and/or enlarging from the pore. Formerly present in: *Triodopsis* (Figs. 9–18). Now present in *Triodopsis vulgata, picea,* and *claibornensis* (Fig. 9).

Discussion. This wall-pustular pattern, in combination with a subterminal pore (Transformation 41), takes on the distinctive appearance of a spider's orb-web (especially Fig. 9a). It is closest to the presumably plesiomorphous pattern seen in the triodopsine outgroups and in *Webbhelix* and *Neohelix,* and could have arisen by fusion and/or simple reduction of wall columns.

Transformation 27—Preceding transformations: 26.

Plesiomorphous state: 15–20 radiating wall columns, all with distinct pustules. Present in (outgroup): *Triodopsis vulgata, picea,* and *claibornensis* (Fig. 9).

Apomorphous state: 15–20 radiating wall columns, the ventral-most with indistinct pustules. Formerly present in *Triodopsis fraudulenta, burchi, tennesseensis, complanata,* and *fulciden* (Figs. 10, 11, 18b). Now present in: *Triosopsis fraudulenta, rugosa* (Fig. 10), *burchi* (Fig. 11a), and *fulciden* (Fig. 18b).

Discussion. The ventral wall columns are semi-smooth, apparently due to either the partial fusion or partial loss of their pustules. Similarity to the indistinct wall pustules of *Webbhelix multilineata* (Fig. 6a) is due to convergence.

Transformation 28—Preceding transformations: 26, 27.

Plesiomorphous state: 15–20 radiating wall columns, the ventral-most with indistinct pustules. Present in (outgroup): *Triodopsis fraudulenta* (Fig. 10), *burchi* (Fig. 11a), and *fulciden* (Fig. 18b).

Apomorphous state: 15–20 radiating wall columns, the ventral-most smooth, with no trace of pustules. Formerly and now present in *Triodopsis tennesseensis* (Fig. 11b, c) and *complanata* (Fig. 11d).

Discussion. The assumption is that the ventral pustules of *tennesseensis* and *complanata* did not become smooth directly, but passed through a semi-smooth stage homologous with that of *fraudulenta, burchi,* and *fulciden.*

Transformation 29—Preceding transformations: 26.

Plesiomorphous state: 15–20 radiating wall columns, the ventral-most unmerging. Present in (outgroup): *Troiodopsis vulgata, picea, claibornensis* (Fig. 9), *burchi, tennesseensis,* and *complanata* (Fig. 11).

Apomorphous state: 15–20 radiating wall columns, the ventral-most merging basally. Formerly present in: all *Triodopsis* except *vulgata, picea, claibornensis, burchi, tennesseensis,* and *complanata* (Figs. 10, 12–18).

Now present in: *Triodopsis fraudulenta, rugosa* (Fig. 10), and *fulciden* (Fig. 18b).

Discussion. The ventral wall columns form spindle shapes by diverging from the pore, then merging basally. The basal merging presumably derived from non-merging columns, probably by a simple change in the developmental program by which the pustular columns form.

Transformation 30—Preceding transformations: 26, 29.

Plesiomorphous state: 15–20 wall columns, the ventral-most merging basally. Present in (outgroup): *Triodopsis fraudulenta, rugosa* (Fig. 10), and *fulciden* (Fig. 18b).

Apomorphous state: all 15–20 wall columns merging midventrally to form a plesiomorphous inverted chevron pattern. Formerly present in: *Triodopsis platysayoides, vultuosa, cragini, henriettae, tridentata, anteridon, juxtidens, discoidea, hopetonensis, palustris, obsoleta, alabamensis, messana, vannostrandi, fallax, soelneri, neglecta,* and *pendula* (Figs. 12–18). Now present in: none.

Discussion: The ventral wall patterns of *platysayoides* (Type 2 chevron) and the remaining species (Type 3 chevron) differ significantly, but have enough features in common that they probably had a common ancestor of unknown appearance, but probably closer to *platysayoides* because of the number of pustular columns involved. It is assumed that the mid-ventral merging of wall columns evolved in a basal-to-apical direction, with an intermediate stage in this process represented by the basal merging seen in *fraudulenta, rugosa,* and *fulciden.* Ontogenetic studies of penial sculpture may prove useful in testing this assumption.

Transformation 31—Preceding transformations: 26, 29, 30.

Plesiomorphous state: all 15–20 wall columns merging midventrally to form a plesiomorphous inverted chevron pattern. Present in (outgroup): hypothesized ancestor probably closest to *Triodopsis platysayoides* (Fig. 12).

Apomorphous state: Type 2 chevron: wall columns all merging midventrally into 10–12 obtuse V-shapes, equilateral, widely separated, and bearing equally sized pustules. Formerly and now present in *Triodopsis platysayoides* (Fig. 12).

Discussion. This Type 2 chevron is convergent on Types 1 and 3 chevrons. For differences from the Type 1 chevron, see the discussion under Transfomation 25. The Type 2 differs from the Type 3 chevron (Transformation 32) by the greater number and more obtuse angle of its ventral V-shapes.

Transformation 32—Preceding transformations: 26, 29, 30.

Plesiomorphous state: all 15–20 wall columns merging midventrally to form an inverted chevron pattern. Present in (outgroup): hypothesized ancestor probably closest to *Triodopsis platysayoides* (Fig. 12).

Apomorphous state: Type 3 chevron: wall columns all merging mid-ventrally into 5–7 acute V-shapes, equilateral, widely separated, and bearing equally sized pustules. Formerly and now present in: *Triodopsis vultuosa, cragini, henriettae, tridentata, anteridon, juxtidens, discoidea, hopetonensis, palustris, obsoleta, alabamensis, messana, vannostrandi, fallax, soelneri, neglecta,* and *pendula* (Figs. 12–18).

Discussion. There is considerable variation within this character state, and a more thorough and extensive study may break it down into a number of systematially useful categories. What is considered the "basic" Type 3 chevron is well represented in the illustrations of *hopetonensis* (Fig. 26a), *palustris* (Fig. 15b), and *alabamensis* (Fig. 16a); it differs from the Type 2 chevron Transformation 31) by the lesser number and the more acute angle of its ventral V-shapes; for its difference from the Type 1 chevron, see the discussion under Transformation 25. Variations from the "basic" Type 3 chevron include the more acutely angled V-shapes, presumably due to penial elongation, in *vultuosa, cragini,* and *henriettae* (Fig. 13); the apparent partial effacement of the wall sculpture of *juxtidens* (Fig. 14c), possibly due to sympatry with the similar *tridentata* (Fig. 14a); the possible effacement of the wall sculpture of *fallax* (Fig. 17a), which may be an artifact of the strong contraction of this specimen; the apparently total effacement of the wall sculpture of *soelneri* (Fig. 17b), possibly due to sympatry with the similar *hopetonensis* (Fig. 15a) and *messana* (Fig. 16b) (see Table 8); and the anastomoses among the V-shapes in *pendula* (Fig. 18c). Deriving both Types 2 and 3 chevrons from a common ancestor is a parsimonious suggestion, but need not be true: the apparent independent origin of the Type 1 chevron is evidence that Types 2 and

3 could have evolved independently of each other as well.

Transformation 33—Preceding transformations: 26, 29.

Plesiomorphous state: 15–20 radiating wall columns, the ventral-most merging basally. Present in (outgroup): *Triodopsis fraudulenta* and *rugosa* (Fig. 10).

Apomorphous state: 8–10 radiating wall columns, the ventral-most merging basally. Formerly and now present in: *Triodopsis fulciden* (Fig. 18b).

Discussion. The wall pattern of *fulciden* is unique and problematic. It most closely resembles *rugosa* (not illustrated, but similar to *fraudulenta* (Fig. 10)), except that the number of pustular columns is approximately halved. This reduction would parallel the reduction in column number suggested in Transformation 32.

Transformation 34—Preceding transformations: none.

Plesiomorphous state: pore flush with the penial wall. Present in (outgroups): some Camaenidae; and Ammonitellidae, *Allogona, Cryptomastix*, and *Triodopsis* (Figs. 9–18).

Apomorphous state: pore ventrally subterminal on a large, apical, dorsoventrally compressed verge which points backward along the everted penis, and with a surface sculpture of cords which continue into 6 or more narrow terminal papillae. Formerly present in: *Webbhelix* (Fig. 6a), *Neohelix* (Figs. 2–6), *Xolotrema* (Figs. 7, 8). Now present in: *Neohelix dentifera, albolabris, alleni, major, lioderma,* and *divesta* (Figs. 2–5).

Discussion. The hypothesized generalized form of the eastern-triodopsine verge is illustrated in dorsal view in Figs. 2a, d, 3a, c, 4a, 5d; and in magnified ventral view, showing the subterminal pore, in Figs. 2f, 3b, 4b, and 4e. The verge of the illustrated specimen of *lioderma* (Fig. 5a, b) is abnormally partially inverted; in undistorted specimens, this species's verge resembles that of *divesta* (Fig. 5d, e). Despite careful search (e.g., Fig. 11c), no trace of a verge was detected in any species of *Triodopsis*—the peduncle (Transformations 45 and 46), despite a superficial resemblance to a verge (e.g. Fig. 14a–d), differs in both position and structural detail. Although Webb's (1961, 1974) hypothesis that *Triodopsis* has secondarily lost the verge cannot be ruled out, this genus's complete lack of any vestige suggests rather that it never had a verge.

Transformation 35—Preceding transformations: 34.

Plesiomorphous state: vergic papillae 6 or more, narrow. Present in (outgroups): *Neohelix* (Figs. 2–5, 6b).

Apomorphous state: vergic papillae 2, broad. Formerly and now present in: *Webbhelix multilineata* (Fig. 6a).

Discussion. Narrow papillae appear to be simple extensions of the basic cord-like substructure of the verge (e.g. Fig. 2f). These cords and papillae are probably homologous with wall-pustular columns. It seems likely that the broad, paired papillae of *multilineata* are derived by fusion of the plesiomorphous narrow papillae. The surface of *multilineata's* verge also appears to be smooth, lacking the cord-like substructure (Fig. 6a).

Transformation 36—Preceding transformations: 34.

Plesiomorphous state: verge large, terminal, longer than wide, bearing 6 or more narrow papillae. Present in (outgroup): *Neohelix dentifera, albolabris, alleni, major, lioderma,* and *divesta* (Figs. 2–5).

Apomorphous state: Type 1 small verge: subterminal and basally-directed, wider than long, bearing 6–8 narrow papillae. Formerly and now present in: *Neohelix solemi* (Fig. 6b).

Discussion. Small size in the eastern-triodopsine verge is correlated with a subterminal position (Types 1 and 3) and with a long penis (slight in Type 3, pronounced in Type 2). Since both a subterminal pore (Character 4) and a long penis (Character 9) seem to be apomorphous conditions (see discussions under Transformations 38–41, 44), small size of the verge may also be apomorphous. In the case of subterminal pore position, this view is supported both by structural differences, indicating convergence, between dorsally subterminal (Type 1) and ventrally subterminal (Type 3) small verges; and by the following theory on functional morphology.

Because the terminal verge of eastern triodopsines unfolds backward during copulation (Webb 1948, 1952, 1954a; see Fig. 1), it is hypothesized that its function is to direct the emitted sperm backward and away from the proteolytic enzymes of the spermathecal bulb. This function seems also to be served, however, by the alternative adaptive "strat-

egy" of moving the pore from a terminal to a subterminal position. Therefore, when the pore becomes subterminal, the verge is no longer functional, and therefore becomes vestigial. This theory, however, does not explain the apparent correlation between a long penis and a short type-2 verge.

Transformation 37—Preceding transformations: 34.

Plesiomorphous state: verge large, terminal, longer than wide, bearing 6 or more narrow papillae. Present in (outgroup): *Neohelix dentifera, albolabris, alleni, major, lioderma,* and *divesta* (Figs. 2–5).

Apomorphous state: Type 2 small verge: terminal, longer than wide, bearing 6 narrow papillae. Formerly and now present in: *Xolotrema fosteri* and *occidentalis* (Fig. 8).

Discussion. Structurally this Type 2 small verge differs from the Type 3 (Transformation 38) only in being longer than wide and in having two more papillae (Fig. 8c vs. Fig. 7b, d), but further comparative study may prove this latter difference insignificant. There is the possibility, therefore, that Types 2 and 3 small verges are homologous, but because of their different positions (terminal vs. subterminal), it is suggested that they have independently become vestigial for functionally different reasons. By similar reasoning, Types 2 and 1 small verges are also convergent.

Transformation 38—Preceding transformations: 34.

Plesiomorphous state: verge large, terminal, longer than wide, bearing 6 or more narrow papillae. Present in (outgroup): *Neohelix dentifera, albolabris, alleni, major, lioderma,* and *divesta* (Figs. 2–5).

Apomorphous state: Type 3 small verge: subterminal and apically directed, wider than long, bearing 4 narrow papillae. Formerly and now present in: *Xolotrema denotata, obstricta,* and *caroliniensis* (Fig. 7).

Discussion. Structurally, this Type 3 small verge (Fig. 7b, d) differs from the Type 1 (Transformation 36) only in having two less papillae, but its vastly different position—ventrally subterminal as opposed to dorsally subterminal—leads to the suggestion that Types 1 and 3 are convergent. The suggested homoplasy Types 3 and 2 is discussed under Transformation 37.

Transformation 39—Preceding transformations: none.

Plesiomorphous state: pore terminal. Present in (outgroups): many Camaenidae; Corillidae, Ammonitellidae, Oreohelicidae; all non-east-American-triodopsine Polygyridae; *Webbhelix;* all *Neohelix* except *solemi; Xolotrema fosteri* and *occidentalis;* and *Triodopsis fraudulenta, burchi, tennesseensis, complanata, platysayoides, vultuosa, cragini, henriettae,* and *fulciden* (Figs. 2–5, 6a, 8, 10–13, 18b).

Apomorphous state: pore dorsally subterminal and on a fleshy pedestal. Formerly and now present in: *Nehoelix solemi* (Fig. 6b).

Discussion. The orientation of the verge and the position of the reduced dorsal pilaster clearly indicate the uniquely dorsal position of the pore in *solemi.*

Transformation 40—Preceding transformations: none.

Plesiomorphous state: pore terminal. Present in (outgroups): many Camaenacea; Corillidae, Ammonitellinidae, Oreohelicidae; all non-eastern-triodopsine Polygyridae; *Webbhelix;* all *Neohelix* except *solemi; Xolotrema fosteri* and *occidentalis;* and *Triodopsis fraudulenta, burchi, tennesseensis, complanata, platysayoides, vultuosa, cragini, henriettae,* and *fulciden* (Figs. 2–5, 6a, 8, 10–13, 18b).

Apomorphous state: Type 1 ventrally subterminal pore: everted penis shaped like an inverted pear, with the pore ca 1/3-way from the apex and on a verge mounted on a fleshy pedestal. Formerly and now present in: *Xolotrema denotata, obstricta,* and *caroliniensis* (Fig. 7).

Discussion. Webb published two illustrations of the everted penis of *denotata* (Webb 1948, Fig. 1a; Webb 1954a, Plate 10, Fig. 11), showing its pyrifom shape and its pore (verge) position. Fig. 7 shows that the dissected, uneverted penis also has this shape, that *obstricta* and *caroliniensis* are essentially identical to *denotata* in this respect, and that the pore is on a fleshy pedestal which is not evident in the everted penis.

Transformation 41—Preceding transformations: none.

Plesiomorphous state: pore terminal. Present in (outgroups): many Camaenidae; Corillidae, Ammonitellinidae, Oreohelicidae; all non-eastern-triodopsine Polygyridae; *Webbhelix;* all *Neohelix* except *solemi; Xolotrema fosteri* and *occidentalis;* and *Triodopsis*

fraudulenta, burchi, tennesseensis, complanata, platysayoides, vultuosa, cragini, henriettae, and *fulciden* (Figs. 2–5, 5a, 8, 10–13, 18b).

Apomorphous state: Type 2 ventrally subterminal pore: everted penis shaped like an angled baseball bat, with the pore ca 1/5-way from the apex and indented into the penial wall. Formerly and now present in: *Triodopsis vulgata, picea,* and *claibornensis* (Fig. 9).

Discussion. Five published illustrations of the everted penis of *vulgata* (Webb 1959, Figs. 22, 27, 34, 38) show the general shape and position of the pore. Fig. 9 (this paper) shows that the dissected, uneverted penis also has this general shape, that *picea* and *claibornensis* are essentially identical to *vulgata* in this respect, and that there is no sign of a pedestal or verge. Webb's figures indicate a sub-pore protuberance ("tubercle") which is covered with pustular columns (Webb 1959, Fig. 38); this is not evident in the uneverted penis (Fig. 9).

Transformation 42—Preceding transformations: none.

Plesiomorphous state: pore terminal. Present in (outgroups): many Camaenidae; Corillidae, Ammonitellinidae, Oreohelicidae; all non-eastern-triodopsine Polygyridae; *Webbhelix;* all *Neohelix* except *solemi; Xolotrema fosteri* and *occidentalis;* and *Triodopsis fraudulenta, burchi, tennesseensis, complanata, platysayoides, vultuosa, cragini, henriettae,* and *fulciden* (Figs. 2–5, 5a, 8, 10–13, 18b).

Apomorphous state: Type 3a ventrally subterminal pore: everted penis shaped like a thick-handled mace, with the pore ca 1/4-way from the apex and above a smooth peduncle. Formerly present in: *Triodopsis juxtidens, discoidea, neglecta,* and *pendula* (Figs. 14c, d; 18a, c). Now present in: *Triodopsis tridentata, anteridon, hopetonensis, palustris, obsoleta, alabamensis, messana, vannostrandi, fallax,* and *soelneri* (Figs. 14a–b, 15–17).

Discussion. Illustrations of the everted penis of four of the ten species with a Type 3a ventrally subterminal pore have been published: *fallax* (Grimm 1975, Fig. 3B), *hopetonensis* (Webb 1959, Figs. 9, 42), *tridentata* (Webb 1948, Fig. 4; Webb 1954a, Fig. 13; Webb 1959, Figs. 14, 28, 35, 40), and *vannostrandi* (Webb 1959, Figs. 17, 25a, 43). Figures 14a–b, 15, 16, and 17 (this paper) show that the dissected, uneverted penes of these four species also have this shape and that the remaining 6 species are essentially identical in this respect.

Transformation 43—Preceding transformations: 42.

Plesiomorphous state: Type 3a ventrally subterminal pore: everted penis shaped like a thick-handled mace, with the pore ca 1/4-way from the apex and above a smooth peduncle. Present in (outgroup): *Triodopsis tridentata, anteridon, hopetonensis, palustris, obsoleta, alabamensis, messana, vannostrandi, fallax,* and *soelneri* (Figs. 14a–b, 15–17).

Apomorphous state: Type 3b ventrally subterminal pore: mace head large, with the pore ca 2/5-way from the apex. Formerly and now present in: *Triodopsis juxtidens* (Fig. 14c), *discoidea* (Fig. 14d), *neglecta* (Fig. 18a), and *pendula* (Flg. 18c).

Discussion. Illustrations of the everted penis of three of these four species have been published: *discoidea* (Webb 1959, Fig. 13), *juxtidens* (Webb 1959, Figs. 15, 41), and *neglecta* (Webb 1959, Figs. 10, 11, 12). Figures 14c, d and 18a, c (this paper) show that in the dissected, uneverted penes of these three species, the Type 3b ventrally subterminal pore is more easily distinguished from the Type 3a by the size of the peduncle (see discussion under Transformation 50) than by the position of the pore, which varies with the state of contraction. Thus, although the pore position of *discoidea* (Fig. 14d) is as it appears in the everted penis, the pores of *juxtidens* (Fig. 14c) and *neglecta* (Fig. 18a) are much closer to the apex than they appear in the everted penes. The pore of *pendula* (Fig. 18c) is intermediate in position and its peduncle is large, so *pendula* is interpreted as having a Type 3b ventrally subterminal pore. Since the Type 3b has a very similar penial shape and sub-pore peduncle to the Type 3a, it is assumed to be homologous and derived from the Type 3a by further overgrowth of the dorsal penial wall, making the terminal knob larger and the pore more subterminal.

Transformation 44—Preceding transformations: none.

Plesiomorphous state: ventral wall free of any pilastral outgrowth. Present in (outgroups): some Camaenidae; Oreohelicidae, Ammonitellidae, and all Triodopsinae except *Neohelix solemi* (Fig. 49).

Apomorphous state: ventral wall bearing a

single pilaster. Formerly and now present in: *Neohelix solemi* (Fig. 6b).

Discussion. Because of its surface sculpture of close, uniform pustules, the ventral pilaster of *solemi* is convergent on the dorsal pilaster of *multilineata* (side-by-side comparison in Fig. 6). It almost certainly is apomorphous.

Transformation 45—Preceding transformations: none.

Plesiomorphous state: 1/3 or less of the total penis length lying between the vaginal opening and the base of the sheath. Present in (outgroups): all eastern Triodopsinae except *Neohelix solemi* (Figs. 2–5, 6a, 7–18).

Apomorphous state: 1/2 or more of the total penis length lying between the vaginal opening and the base of the sheath. Formerly and now present in: *Neohelix solemi* (Fig. 6b).

Discussion. A long basal penis occurs in the polygyrid ashmunellines *Cryptomastix, Allogona,* and *Ashmunella,* but it appears that this character state in *Neohelix solemi* is not homologous because of its absence in *solemi's* more immediate outgroup, the remaining species of *Neohelix.*

Transformation 46—Preceding transformations: none.

Plesiomorphous state: mid-ventral wall free of sperm groove. Present in (outgroup): all eastern triodopsines except *Xolotrema fosteri* and *occidentalis* (Figs. 2–7, 9–18).

Apomorphous state: mid-ventral sperm groove present. Formerly and now present in: *Xolotrema fosteri* and *occidentalis* (Fig. 19).

Discussion. The term "ventral sperm groove" refers to the smooth, mid-ventral, raised channel shown (somewhat exaggeratedly) in Fig. 8a, b, and shown in cross section in Pilsbry (1940, Fig. 473 #7b), even though its function is unknown. It is not conspicuous in any of Webb's illustrations of the everted penis of *fosteri* (Webb 1952, Figs. 6, 8, 10, 11; Webb 1954a, Fig. 12), but is pronounced enough in the dissected, uneverted penis to be mistaken for the dorsal pilaster—transverse folds across the sperm groove in a contracted specimen of *occidentalis* (Fig. 8b) even produce a superficial resemblance to pilastral lappets (e.g., Fig. 2d).

Transformation 47—Preceding transformations: none.

Plesiomorphous state: sheath covering 1/2 or less of the upper penis. Present in (outgroup): all eastern triodopsines except *Xolotrema fosteri* and *occidentalis* (Figs. 2–7, 9–18).

Apomorphous state: sheath covering the entire upper penis. Formerly and now present in: *Xolotrema fosteri* and *occidentalis* (Fig. 8).

Discussion. Penial sheath length varies a great deal depending on the preservational state of the individual snail, so no attempt was made to analyze interspecific differences, with the single exception of this distinct and obviously apomorphous character state. The apparently long sheath of the illustrated specimen of *Neohelix dentifera* (Fig. 2a) resulted from prolapse of the upper penis into the basal penis, evidenced by the pattern of folds at the upper-basal junction—in other dissected specimens of *dentifera* the sheath appeared relatively shorter. The illustrated penis of *X. fosteri* (Fig. 8a) appears to be normal in length, but that of *X. occidentalis* (Fig. 8b) is obviously contracted within its uncontracted sheath.

Transformation 48—Preceding transformations: none.

Plesiomorphous state: upper penis short to long. Present in (outgroup): all eastern triodopsines except *Triodopsis vultuosa, cragini,* and *henriettae* (Figs. 2–12, 14–18).

Apomorphous state: upper penis extremely long and thread-like. Formerly and now present in *Triodopsis vultuosa, cragini,* and *henriettae* (Fig. 13).

Discussion. The length of the upper, pustulated, penis is subject to some individual variation depending on preservational state. Because of this, and because of the high probability of convergence in such a developmentally plastic character as overall length, penial length was not considered for systematic analysis except in this extreme and obviously apomorphous case. The everted penis (illustrated in Webb 1959, Figs. 26b, 26c, 32; and Grimm 1975, Fig. 3c) is conspicuously long and narrow.

Transformation 49—Preceding transformations: none.

Plesiomorphous state: sub-pore region flat or gradually raised. Present in (outgroup): *Webbhelix; Neohelix; Xolotrema;* and *Triodopsis vulgata, picea, claibornensis, fraudulenta, burchi, tennesseensis, complanata, platysayoides, vultuosa, cragini, henriettae,* and *fulciden* (Figs. 2–13, 18b).

Apomorphous state: sub-pore region erectile as a small, fleshy peduncle. Formerly

present in: *Triodopsis juxtidens, discoidea, neglecta,* and *pendula* (Figs. 14c, d; 18a, c). Now present in: *Triodopsis tridentata, anteridon, hopetonensis, palustris, obsoleta, alabamensis, messana, vannostrandi, fallax,* and *soelneri* (Figs. 14a–b, 15–17).

Discussion. The peduncle was defined by Webb (1959) as the smooth, fleshy knob just beneath the subterminal pore in the everted penis of *hopetonensis, tridentata, vannostrandi, discoidea, juxtidens,* and *neglecta.* It occurs in two disjunct sizes: small and large. In neither of these is there any substructural detail suggesting homology with the verge, so independent derivation is assumed, with the large peduncle derived from the small peduncle. The sub-pore "tubercle" of *vulgata* (Webb 1959) is not smooth but pustulose and is not a distinct knob, so probably is not homologous with the peduncle. The peduncle appears to consist of erectile tissue which variously appears in the dissected, uneverted penis as a lobe (Fig. 14a, b, c, d), thickened region (Figs. 15a, c; 16b; 17a, b), or wrinkled sac (Figs. 15b; 16a, c; 18a, c) beneath the pore. The erect small peduncle is best illustrated in Webb 1948, Fig. 4 (as the "protuberance"), and in Webb 1959, Figs. 14, 25a, 40, and 43.

Transformation 50—Preceding transformations: 49.

Plesiomorphous state: peduncle small. Present in (outgroup): *Triodopsis tridentata, anteridon, hopetonensis, palustris, obsoleta, alabamensis, messana, vannostrandi, fallax,* and *soelneri* (Figs. 14a–b, 15–17).

Apomorphous state: peduncle large. Formerly and now present in: *Triodopsis juxtidens, discoidea, neglecta,* and *pendula* (Figs. 14c, d; 18a, c).

Discussion. The erect large peduncle is best illustrated in Webb 1959, Figs. 12, 13, 15, and 41. The large peduncle can be distinguished from the small peduncle in the dissected, uneverted penis by its large size, whether it is inflated (Fig. 14c, d) or deflated (Fig. 18a, c).

Cladistic analysis

The presence or absence of each of the 50 suggested anatomical transformations in each species of eastern triodopsines is presented in Table 1.

To simplify cladistic analysis, genitalically identical species were pooled, reducing the number of operational taxa from 40 species to 18 groups (Table 1). Nine of these groups consisted of a single species *(W. multilineata, N. solemi, N. albolabris, N. major, N. alleni, T. picea, T. fulciden, T. burchi,* and *T. platysayoides).* Each of the remaining multispecies groups was temporarily named for one of its better-known species without regard for previously named supraspecific taxa. By far the largest of these (Table 1) was the *T. tridentata* group, comprising 10 species *(tridentata, anteridon, fallax, obsoleta, palustris, messana, soelneri, alabamensis, vannostrandi,* and *hopetonensis).* One of these, *soelneri,* was problematic in that it lacks wall pustules and its pilaster lacks surface sculpture (Fig. 17b). However, because of its Type 3a ventrally subterminal pore, its small peduncle, and the basic similarity of its pilaster to a *tridentata*-type without the conical processes, *soelneri* was considered a highly derived member of the *tridentata* group. The remaining 8 multi-species groups were nonproblematic. The *N. dentifera* group had three species *(dentifera, divesta,* and *lioderma);* the *X. fosteri* group had two species *(fosteri* and *occidentalis);* the *X. denotata* group had three species *(denotata, obstricta,* and *carolinienses);* the *T. vulgata* group had two species *(vulgata* and *claibournensis);* the *T. fraudulenta* group had two species *(faudulenta* and *rugosa);* the *T. tennesseensis* group had two species *(tennesseensis* and *complanata);* the *T. cragini* group had three species *(cragini, vultuosa,* and *henriettae);* and the *T. juxtidens* group had four species *(juxtidens, discoidea, neglecta,* and *pendula).*

Cladistic analysis resulted in a single most parsimonious tree (Fig. 24) with convergences in three transformations and with no reversals (consistency index = 48.5/50 = .970). The three convergences were in transformations 27, 29, and 30. The convergence in 27 was biologically probable, because two easily identifiable convergences were already known for this character (Transformations 22 and 23). Convergences in 29 and 30 were also not unreasonable, as had been noted in the discussion of Transformation 31. The most parsimonious way to avoid these two homoplasies involved an alternative placement of *T. platysayoides.* This alternative produced a tree with an overall consistency index only slightly lower (48/50 = .960), but it invoked three reversals in the *T. platysayoides* lineage (Transformations 16, 19, and 21). This was clearly an inferior alternative to

TABLE 1. Presence (1) or absence (0) of 50 hypothesized character-state transformations in each of the 40 species of eastern American triodopsines. The 18 groups consist of species with identical presence/absence patterns.

Temporary species group	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
—	OUTGROUPS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
multilineata	*multilineata*	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
solemi	*solemi*	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0
albolabris	*albolabris*	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
major	*major*	1	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
alleni	*alleni*	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
dentifera	*dentifera*	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
dentifera	*divesta*	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
dentifera	*lioderma*	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
fosteri	*fosteri*	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
fosteri	*occidentalis*	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
denotata	*denotata*	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
denotata	*obstricta*	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
denotata	*caroliniensis*	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
vulgata	*vulgata*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
vulgata	*claibornensis*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
picea	*picea*	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
fraudulenta	*fraudulenta*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
fraudulenta	*rugosa*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
fulciden	*fulciden*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
tennesseensis	*tennesseensis*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
tennesseensis	*complanata*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
burchi	*burchi*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
platysayoides	*platysayoides*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
cragini	*cragini*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
cragini	*vultuosa*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
cragini	*henriettae*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
tridentata	*tridentata*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
tridentata	*anteridon*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
tridentata	*fallax*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
tridentata	*messana*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
tridentata	*palustris*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
tridentata	*obsoleta*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
tridentata	*soelneri*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
tridentata	*alabamensis*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
tridentata	*vannostrandi*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
tridentata	*hopetonensis*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
juxtidens	*juxtidens*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1
juxtidens	*discoidea*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1
juxtidens	*neglecta*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1
juxtidens	*pendula*	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1

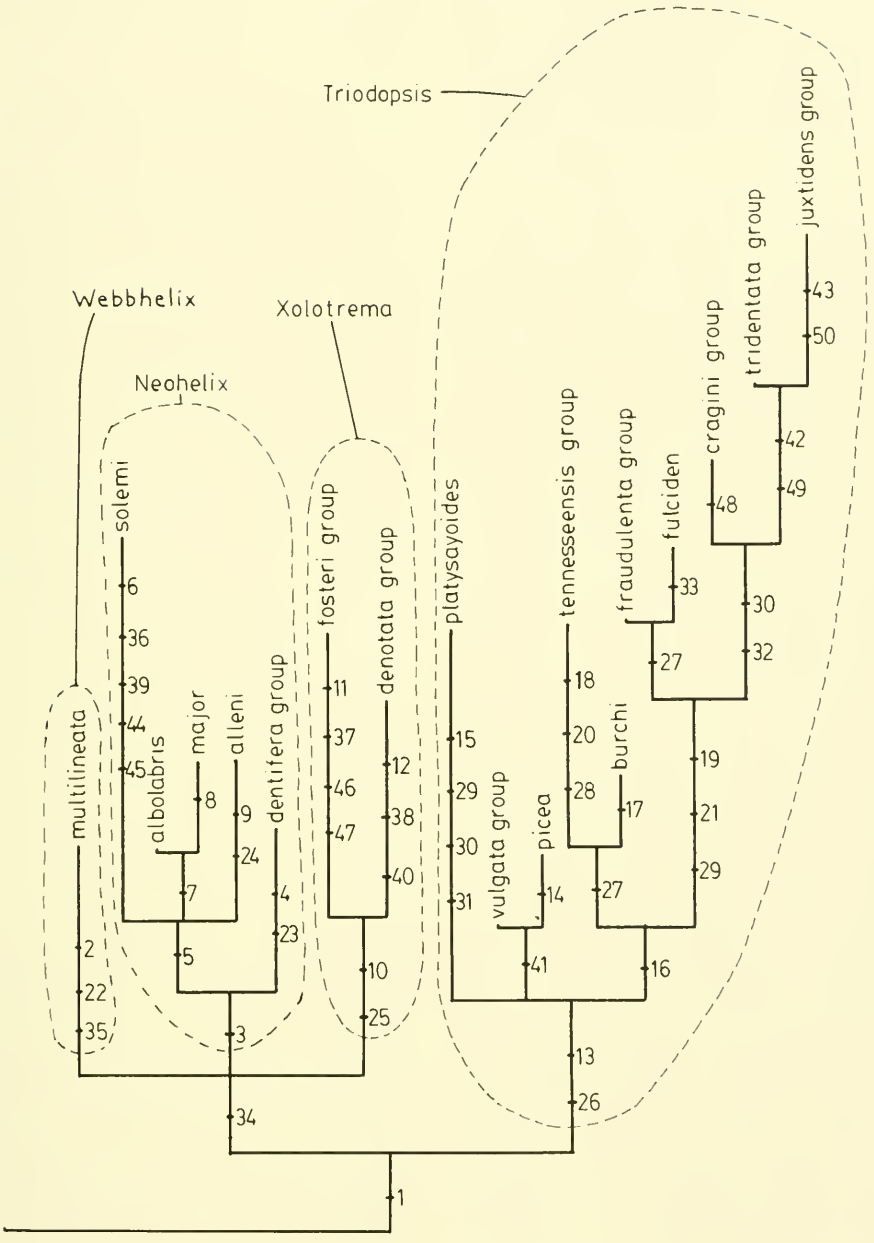

FIG. 24. "Anatomy Tree": a phylogenetic hypothesis for the eastern American triodopsines based on penial morphology (50 character-state transformations shown in Figs. 19–23). This is the single most parsimonious tree generated by PAUP, with a consistency index of .970.

having convergences in Transformations 29 and 30, so Fig. 24 was decidedly the best cladogram to fit the data.

Thus Fig. 24 is the "Anatomy Tree". The branch lengths of this cladogram are scaled to the number of transformations they contain, so are a rough indicator of the degree of evolutionary change in penial morphology.

ALLOZYMIC ANALYSES

Complete electrophoretic results are presented in Table 2. In this table, each allele (electromorph) is represented by its migration distance on the gel in mm relative to the control (*Mesodon zaletus* from Monte Sano, Alabama: FMNH 214772 and 214773), the migration distance of which was arbitrarily set at 100 mm. Seventy-four alleles were detected in the eastern triodopsines and 9 in the outgroup *Allogona profunda*. The most variable loci were Lap and Pgm, with 12 and 11 alleles. Sordh and Me each had 8 alleles; Icd had 7; Gpi had 5; Mdh-1, Mdh-2, Gd-1, Gd-2, and Sod-1 each had 4; Sod-2, Got-2, and Mpi each had three; Got-1 had two; and Pgd was the only monomorphic locus.

Heterozygosity within populations was extremely low. Most populations were monomorphic for all but two or three loci, with a maximum of three alleles per locus (Table 2).

Twenty triodopsine alleles were absent from the outgroup *Mesodon* and therefore were presumed apomorphous. The distributions of these alleles among triodopsine species are listed in Table 3. Twelve alleles were restricted to a single species; the remaining 8 were present in two to 10 species.

Phylogenetic analysis produced the "Alleles Tree" presented in Fig. 25. This cladogram is the consensus of the first 50 trees with a maximum, identical consistency index generated by PAUP; its numbered transformations refer to the alleles listed in Table 3. The Alleles Tree contains one convergence (Lap_{94} between *picea* and *tennesseensis*) and one reversal (loss of Icd_{98} in *hopetonensis*). Comparison of 50 trees showed that both this homoplasy and this reversal are robust, occurring in 100% and 88% of the trees respectively.

Phenetic analyses of the two independent subsets of the allozymic data are presented in Figs. 26 and 27. The first of these, the "Wagner-1 Tree", comprising 32 species evaluated over 16 loci, has a cophenetic correlations of .897, indicating only mild distortion of the original genetic distance matrix. The "Wagner-2 Tree" (21 species, 8 loci) has a similarly high cophenetic correlation of .883.

CONSENSUS PHYLOGENY

To aid in comparing the Anatomy Tree (Fig. 24), the Alleles Tree (Fig. 25), the Wagner-1 Tree (Fig. 26), and the Wagner-2 Tree (Fig. 27), each was labeled in a consistent manner: genera and outgroups were enclosed by dashed lines.

The trees were weighted for comparison. In the Anatomy Tree, 3 out of the 50 transformations (.06) showed reversal or convergence, whereas the Alleles Tree had 2 out of 20 (.10). Dividing these gave a "reliability" of anatomical over allozymic data units of 1.6. The number of data units for each tree was: Anatomy 50, Alleles 20, Wagner-1 73, and Wagner-2 28. Multiplying the morphological data units by 1.6 and dividing all by 75 and rounding gave the following weights: 1.0 for the Anatomy Tree, 0.3 for the Alleles Tree, 1.0 for the Wagner-1 Tree, and 0.4 for the Wagner-2 Tree.

The four genera—*Neohelix, Triodopsis, Webbhelix,* and *Xolotrema*—are distinct and coherent throughout all four Trees (Figs. 24–27). The four minor exceptions to this general pattern are readily resolved. (1) In the Alleles Tree, *N. albolabris* appears in *Triodopsis* due only to the presence of Icd_{98} (Transformation 10) in one of its three populations (*albolabris*-2), which could easily be a homoplasy. (2) Also in the Alleles Tree, *T. messana* is grouped in *Neohelix* due only to its possession of Icd_{96} (Transformation 11), which could be a homoplasy. (3) In the Wagner-1 Tree, *T. burchi* groups within *Neohelix;* in the equally weighted Anatomy Tree, however it pairs with the *T. tennesseensis* group, well within *Triodopsis,* and the occurrence of this pairing in the Alleles Tree gives it greater weight than a *Neohelix* position for *T. burchi;* its genetic similarity to *Neohelix* could be due either to homoplasy in alleles or to retention of plesiomorphous alleles. (4) The isolated position of *X. fosteri* within *Neohelix* in the Wagner-2 Tree (weight 0.4) is outweighed by its firm position within *Xolotrema* in both the Anatomy and Alleles Trees (combined weight 1.3); *X. fosteri* does not occur in the Wagner-1 Tree. With these

exceptions resolved, there remains no doubt of the robustness of the four genera.

Neohelix, Webbhelix, and *Xolotrema* together constitute a monophyletic group, according to the Anatomy Tree and both Wagner Trees. According to the Wagner-1 Tree, *Webbhelix* is the most plesiomorphous genus; in both the Anatomy and Alleles Trees, it is concordant with *Neohelix* and *Xolotrema,* but retains more plesiomorphous charcter-states than either of these genera. This combined evidence that *Webbhelix* is the most plesiomorphous genus of eastern triodopsines outweighs the Wagner-2 Tree's placement of it as sister group to *Xolotrema.*

The grouping of *Neohelix albolabris, N. major, N. alleni,* and the highly derived *N. solemi* in the Anatomy Tree receives enough verification in the two Wagner Trees for acceptance as it stands. In the Wagner-1 Tree, *alleni, major,* and *solemi* cluster together but are isolated from *albolabris.* However, in the Wagner-2 Tree, *albolabris* (two populations) does cluster with *alleni* (three populations) and *major* (two populations), but this cluster is isolated from a single population of *alleni* (*alleni*-4); *solemi* is missing from this tree. Thus, except for one slightly errant population in each of the two Wagner Trees, the evidence is consistent for an *albolabris-major-alleni-solemi* cluster, with *solemi* the most highly derived member both anatomically (Fig. 24) and electrophoretically (Fig. 26) as indicated by its long branch length in each of these trees. These four species comprise the *Neohelix albolabris* group, which is revised in the following section.

The *Neohelix dentifera* group *(dentifera, divesta,* and *lioderma)* is clearly coherent and isolated from the other *Neohelix* anatomically (Fig. 24) and electrophoretically (Figs. 26, 27). There is no evidence in any of these trees as to the relationships of the three species within the group, but *dentifera* appears to have a less apomorphous form of enlarged basal pustules, as discussed under anatomical Transformation 4, so may be plesiomorphous within the group. The *dentifera* group's position primitive to the *albolabris* group is evident in the Anatomy, Wagner-1, and Wagner-2 Trees, and is only contradicted by *alleni* and *lioderma* sharing Icd_{96} (Transformation 11) in the Alleles Tree, which could easily be a convergence and is strongly outweighed by the evidence of the other trees.

The anatomical division of *Xolotrema* (Fig. 24) into the *fosteri* group *(fosteri* and *occidentalis)* and the *denotata* group *(denotata, obstricta,* and *caroliniensis)* is only partially supported by the electrophoretic data. The pair *denotata* and *obstricta* is linked by a unique derived allele (Me_{108}) in the Alleles Tree (Fig. 25) and is also tightly linked in both Wagner Trees (Figs. 26, 27), but *caroliniensis* groups no closer to this pair than does *fosteri* in the Alleles Tree or *occidentalis* in both Wagner Trees. However, since *caroliniensis* is represented electrophoretically by only a single specimen (Table 2), its relative position in these trees should not be considered very precise. Complete electrophoretic data were lacking for *fosteri* (Table 2), so it does not occur in the Wagner-1 Tree. In the Wagner-2 Tree, *fosteri* is strongly isolated not only from *occidentalis* but from the remainder of *Xolotrema* in general, but this placement based on genetic distance is shown cladistically to be aberrant in the Alleles Tree: *fosteri* shares one derived allele, ($Sordh_{98}$) with the remainder of *Xolotrema* and another derived allele (Me_{105}) with the *denotata* group. The Alleles Tree also shows that *occidentalis* is separated from *fosteri* by its lack of Me_{105} and its unique possession of Gpi_{107}.

Despite these partial discrepancies with the electrophoretic trees, the anatomical disjunction between the *fosteri* and *denotata* groups is so extreme (seven transformations in the anatomy Tree) and the penial sculpture within each of these two groups is so cohesive (Figs. 7 and 8), that there can be no doubt of their separation. The fact that there has been little electrophoretic differentiation between the *fosteri* and *denotata* groups suggests that their anatomical distinctions have evolved relatively recently. There is no clear evidence from any of the trees as to which of these two groups is the more plesiomorphous.

Within *Triodopsis* there are some discrepancies among the four trees of such magnitude that the original dissections were reexamined and several interpretive errors were detected. The Consensus Tree (Fig. 28), therefore, differs from the Anatomy Tree (Fig. 24) more for this genus than for any other, and contains some redefinitions of species groups.

In the Wagner-1 Tree (Fig. 26), the *T. vulgata* group *(vulgata* and *claibornensis), T. picea,* the *T. fraudulenta* group (*fraudulenta* and *rugosa,* but represented only by *fraudulenta*), and *T. platysayoides* form a single, shallowly rooted group with no differentiation into subgroups except for a shallow pairing of

TABLE 2. Allozyme data for 64 populations comprising 35 species of eastern American triodopsines, plus two populations of the outgroup *Allogona profunda*. Not shown in the table is a 16th locus, Pgd, for which all populations were monomorphic at 100.

Species	FMNH catalogue number	N	Locus														Total alleles
			Sordh	Mdh-1	Mdh-2	Me	Icd	Gd-1	Gd-2	Sod-1	Sod-2	Got-1	Got-2	Pgm	Lap	Mpi	Gpi	
Allogona profunda	—	10	94	107	100(.20) 95(.80)	104	90	103(.10) 99(.90)	99	110(.05)	100	100	97	98(.15) 95(.75) 86(.10)	105(.85) 102(.10) 98(.05)	100	104(.70) 100(.30)	
T. alabamensis	214791	6	102	96	100	100	100	102	98	90	100	100(.58) (.42)	97	103(.08) 99(.84) 97(.08)	99 99	102 102	104(.08) 100(.75) 95(.17)	
N. albolabris	214920	5	103	91	100	100	100	103	99	90	107	100	97	95(.80) 91(.20)	99(.20) 97(.80)	100	100	
N. alleni	214911	6	103(.58) 101(.17) 89(.25)	91	100	100	96	103	99	100	107	100	97	99(.58) 97(.42)	99	100	100	
T. anteridon	214793	3	102	96	100	99	98	102	99	100(.67) 90(.33)	100	100	97	99(.33) 97(.67)	97	102	104(.17) 100(.83)	
T. burchi	214797	6	102	96	100	102	100	102	99	100	107	100	97	102(.75) 100(.25)	97	100	100	
X. caroliniensis	—	1	98	91	99	105(.50) 100(.50)	103	103	99	90	107	100	97	97	102	100	100	
T. claibornensis	214800	4	101	96	100	100	98	102	99	100(.88) 90(.12)	100	100	97	97(.50) 95(.50)	99	102	100	
T. complanata	214802	2	101	96	100	102	100	102	99	90	100	100	97	99(.75) 97(.25)	97	102	104(.50) 100(.50)	
T. cragini	214803	6	102	96	100	100	102	102	99	90	100	97	97	99	97	100	100(.08) 95(.92)	
X. denotata	214806	9	98	91	99	108(.06) 105(.94)	103	103	100	90	107	100	97	97(.94) 95(.06)	102(.06) 100(.22) 97(.72)	100	104(.06) 100(.94)	
N. dentifera	214809	5	102	96	100	100	102	103	99	100	107	100	97	97(.10) 95(.50) 91(.40)	97(.40) 95(.60)	96	100	
N. divesta	214814	5	102	96	100	100(.70)	100	103	99	100	107	100	97	97	99	96	100	
T. fraudulenta	214822	6	102	96	99.5	104(.83) 100(.17)	98	102	100	100(.50) 90(.50)	107(.33) 10(.67)	97	97	97(.08) 95(.92)	99(.08) 97(.75) 95(.17)	100(.92) 96(.08)	100	
T. hopetonensis	—	4	102	96	100	98	100	102	100	90	100	100	97	75	98	102	104(.75) 100(.25)	
T. juxtidens	214842	5	100	96	100	98	98	102	100	100(.10) 90(.90)	100	100	97	97	99(.80) 97(.20)	102	104(.50) 100(.50)	
N. lioderma	214844	10	100	96	100	97	96	103	99	100	107	100	97	97(.15) 95(.85)	99	96	100	
N. major	214930	5	103	91	100	100	100	103	99	100	107	100	97	98(.50) 95(.50)	99(.90) 97(.10)	100	100	
T. messana	214846	4	102	96	100	100	96	102	99	90	100	100(.88) (.12)	97	97(.75) 95(.25)	97	102	104(.25) 100(.75)	
W. multilineata	214849	3	102	91	99	100	100	101	100	100	100	100	97	98	100	96	99	
T. neglecta	214850	5	102	96	100	98	100	102	98	100(.10)	100	100	105(.30) 97(.70)	100(.20) 98(.70) 91(.10)	99(.10) 97(.90)	102(.20) 100(.80)	100	

X. obstricta	214854	5	98	91	99	108(.10) 105(.90)	103	103	100	90	107	100	97	99(.10) 97(.70) 95(.20)	97	100	104(.10) 100(.90)
X. occidentalis	214856	5	98	91	99	100	103	103	100	90	107	100	97	97	95	100	107(.80) 100(.20)
T. palustris	214857	5	102	96	100	100	100	102	99	90	100	100	97	100(.20) 98(.40) 95(.40)	99(.70) 97(.30)	102(.50) 100(.50)	100
T. pendula	214859	4	102(.88) 100(.12)	96(.25) 91(.75)	100	98	98	102	100	90	100	100	97	75	100(.88) 99(.12)	102	100
T. picea	214860	5	102	91	100	104(.70) 100(.10) 98(.20)	98	102	100	100	107(.30) 100(.70)	100(.10) 97(.90)	97	100(.10) 97(.70) 95(.20)	97(.10) 94(.40) 92(.50)	102	100
T. platysayoides	214861	4	101	96	100	100	102	102	98	100	100	97	97	97(.62) 95(.38)	97	102	100
N. solemi	214943	3	101.5	91	100	100	100	103	99	100	106	100	97	98(.50) 95(.50)	97	100	95
T. tennesseensis	214864	3	101	96	100	102	100	102	99	100(.17) 90(.83)	100	100(.83) 97(.17)	97	100(.17) 97(.66) 95(.17)	97(.33) 94(.67)	102	100
T. tridentata	214876	4	101	96	100	99	100	102	100	90	100	100	97	98(.12) 96(.88)	99	102	100
T. vannostrandi	214880	7	102	96	100	98	98	102	99	100(.07) 90(.93)	107(.07) 100(.93)	100	97	97(.21) 95(.79)	100(.86) 98(.14)	102	100(.71) 95(.29)
T. vulgata	214884	7	101	96	100	104(.07) 100(.86) 98(.07)	98	102	100	100(.64) 90(.36)	100	100	100(.36) 97(.64)	98(.43) 95(.57)	98(.93) 89(.07)	102	100(.79) 95(.21)
T. vultuosa	214887	3	102	96	100	98	102	102	99	90	100	97	97	103(.66) 100(.17) 99(.17)	98	102	100(.50) 95(.50)
Allogona profunda—2	—	2	94	107	100(.50) 95(.50)	104	90	—	—	99	—	100	—	91(.75) 86(.25)	—	100	104(.25) 100(.75)
N. albolabris—2	—	2	103	96(.25) 91(.75)	100	100	98	—	99	90	107	100	97	95(.75) 91(.25)	97	—	100
N. albolabris—3	214919	4	103	96	100	100	100	103	99	100(.37) 90(.63)	107	100	97	95	99	102	100
N. alleni—2	214908	1	100	96	100	100	—	—	—	100	107	100	97	95	—	100	100
N. alleni—3	214909	1	100	96	100	100	—	—	—	100	107	100	97	95	—	100	100
N. alleni—4	—	12	102	96	100	100	100	103	100	100	107	100	100	97	99	100	100
N. alleni—5	214910	5	103(.70) 101(.20) 89(.10)	96(.10) 91(.90)	100	100	96	103	98	100(.75) 90(.25)	107	100	97	97(.60) 95(.30) 91(.10)	99(.60) 96(.40)	100	104(.20) 100(.80)
T. anteridon—2	214796	2	102	96	100	99	98	102	99	100(.75) 90(.25)	100	100	97	99(.25) 97(.75)	97	100	100
T. cragini—2	214804	3	102	96	100	100	100	102	99	90	100	100	97	97(.50) 95(.50)	97	102	100
X. denotata—2	214805	2	98	91	99	105	—	—	—	90	107	100	—	97	—	100	104(.25) 100(.75)
N. dentifera—2	214810	1	102	96	100	100	102	103	99	90	107	100	97	95	97(.50) 95(.50)	96	100
N. divesta—2	214813	2	102	96	100	100	100	103	99	100	107	100	97	95	99(.75) 96(.25)	96	100

TABLE 2. (Continued)

Species	FMNH catalogue number	N	Locus														Total alleles
			Sordh	Mdh-1	Mdh-2	Me	Icd	Gd-1	Gd-2	Sod-1	Sod-2	Got-1	Got-2	Pgm	Lap	Mpi	Gpi	
*X. fosteri	214819	10	98	96	100	105(.45) 100(.55)	100	—	—	100	—	100	97	97(.25) 95(.25) 91(.50)	97	100	100	
*T. fulciden	214823	2	102	96	100	104	98	—	—	90	100	100	97	103(.50) 100(.50)	101(.75) 98(.25)	102	95	
*T. henriettae	214824	2	102	96	100	98	104(.75) 102(.25)	—	—	90	100	97	97	100(.50) 98(.50)	98	102	95	
T. hopetonensis—2	214832	1	102	96	100	98	100	102	100	90	100	100	97	75	98	102	100	
T. juxtidens—2	214840	2	101	96	100	98	98	102	100	90	100	100	97	100(.50) 97(.50)	99	102	100	
N. major—2	214928	3	103	91	100	100	100	103	97	100	107	100	97	98(.33) 95(.67)	97	102(.17) 100(.83)	100	
N. major—3	214927	7	103	96(.79) 91(.21)	100	100(.30) 98(.70)	100	103	99	100	107	100	100	95	97	100	100	
W. multilineata—2	214848	1	102	91	99	100	100	—	100	100	107	100	97	98	100	96	100	
X. obstricta—2	214852	1	98	91	99	100	—	—	—	90	—	100	—	97(.50) 95(.50)	—	100	100	
X. obstricta—3	214853	1	98	96	99	100	—	—	—	90	—	100	—	97(.50) 95(.50)	—	100	104	
X. occidentalis—2	214855	2	98	91	99	100	103	103	100	100(.50) 90(.50)	107	100	97	97	95	100	100	
T. palustris—2	214858	2	102	96	100	100	100	102	99	90	100	100	97	100(.25) 98(.50) 95(.25)	99(.50) 97(.50)	102	100	
T. tennesseensis—2	214865	2	101	96	100	102	100	102	99	90	100	100	97	100(.75) 95(.25)	94	102	100	
T. tridentata—2	—	2	101	96	100	99	—	—	—	90	—	100	—	99(.25) 97(.50) 95(.25)	—	—	100	
T. tridentata—3	214866	1	101	96	100	100	102	—	99	100(.50) 90(.50)	100	100	97	98(.50) 96(.50)	96	97	100	
T. tridentata—4	214878	3	101	100(.17) 96(.83)	100	99	103(.33) 100(.67)	102	99	100(.17) 90(.83)	100	100	97	99(.50) 97(.50)	99(.83) 97(.17)	102	100	
T. tridentata—5	214867	1	101	96	100	—	100	—	—	90	100	100	97	97	97	100	100	
T. tridentata—6	—	9	101	96	100	—	100	—	—	90	100	100	97	99(.44) 97(.56)	97	100	100	
T. vulgata—2	214885	3	101	96	100	100	98	102	100	100(.67) 90(.33)	100	100(.83) 97(.17)	100(.67) 97(.33)	98(.33) 95(.67)	98	102	104(.17) 100(.83)	
T. vultuosa—2	—	2	102	96	100	98	102	102	99	90	100	97	97	97(.50) 95(.50)	98	102	100(.50) 95(.50)	
T. vultuosa—3	—	2	102	96	100	98	102	102	99	90	100	97	97	103(.75) 100(.25)	98	102	100(.50) 95(.50)	
Total Alleles: Triodopsines			7	3	3	8	6	3	4	2	3	2	3	10	11	3	5	73
Allogona only			1	1	1	0	1	1	0	2	0	0	0	1	1	0	0	9
Total			8	4	4	8	7	4	4	4	3	2	3	11	12	3	5	82

TABLE 3. Alleles in eastern American triodopsines which are considered apomorphous (i.e., absent from their outgroup *Mesodon*), and the species in which they were detected.

Locus	Allele	Species
1. Sordh	101.5	*solemi*
2. Sordh	98	*caroliniensis, denotata, fosteri, obstricta, occidentalis*
3. Sordh	89	*alleni*
4. Mdh-2	99.5	*fraudulenta*
5. Me	108	*denotata, obstricta*
6. Me	105	*caroliniensis, denotata, fosteri, obstricta*
7. Me	102	*burchi, complanata, tennesseensis*
8. Me	97	*lioderma*
9. Icd	104	*henriettae*
10. Icd	98	*albolabris, anteridon, claibornensis, fulciden, juxtidens, pendula, picea, vannostrandi, vulgata*
11. Icd	96	*alleni, lioderma, messana*
12. Gd-1	101	*multilineata*
13. Gd-2	97	*major*
14. Sod-2	106	*solemi*
15. Got-2	105	*neglecta*
16. Pgm	96	*tridentata*
17. Pgm	75	*hopetonensis, pendula*
18. Lap	94	*picea, tennesseensis*
19. Gpi	107	*occidentalis*
20. Gpi	99	*multilineata*

fraudulenta and *picea.* This pattern contrasts strongly with that seen in the Anatomy Tree (Fig. 24), in which the *fraudulenta* group plus *fulciden* is quite isolated from the *vulgata* group, *picea,* and *platysayoides,* with the *tennesseensis* group plus *burchi* intervening. Selected dissections of *vulgata, picea, fraudulenta, rugosa, fulciden,* and *platysayoides* were repinned and compared. It was found that Fig. 10 misrepresents the pilastral structure of *fraudulenta,* which is actually much more like that of *picea* (Fig. 9b), but is variable within a single population (FMNH 214822), with some individuals (e.g. #6) showing secondary fusion of pustules which only superficially resembles the knob-less, spurred pilastral polygons of the *tridentata, juxtidens,* and *cragini* groups. Also, the pore of *fraudulenta* is Type-2 ventrally subterminal, which, in retrospect, is apparent in Fig. 10. Thus, *fraudulenta* is actually anatomically closest to *picea,* and the basal merging of its ventral-most wall columns is homoplasic with this condition in *rugosa* and *fulciden,* which have the *tridentata*-like, rather than the *picea*-like pilastral sculpture, and which still appear to have a terminal pore. This dissolves the previous *fraudulenta* group *(fraudulenta* and *rugosa)* of Table 1 and Figs. 24–27, leaving *rugosa* by itself, and redefines a new two-species *fradulenta* group as *picea* and *fradulenta,* with *fraudulenta* its most derived member, and closest anatomically to the *vulgata* group. On re-inspection, it appears that *platysayoides's* unique pilastral sculpture could be directly evolved from the more undifferentiated sculpture of the pilaster *vulgata* and *claibornensis,* as was anticipated in the discussion of Transformation 15. These revised anatomical decisions are reflected in the positions of the (revised) *vulgata* group and *platysayoides* in Fig. 28, which, unlike the Anatomy Tree (Fig. 24), is compatible with the Wagner-1 Tree (Fig. 26). Only one of these reconsidered species *(vulgata)* occurs in the Wagner-2 Tree (Fig. 27), and its pairing there with *tridentata* is at variance with the consensus reached in Fig. 28, but carries little relative weight. The Alleles Tree (Fig. 25) offers no strong contradiction to the Consensus Tree's arrangement of the *vulgata* group (it lacks *platysayoides*), for *fraudulenta* only lacks one allele (Icd_{98}) which is shared by *vulgata, picea,* and *claibornensis,* and the value of this allele is apparently lessened by its patchy distribution among members of the *tridentata* and *juxtidens* groups as well.

The *T. tennesseensis* group *(tennesseensis* and *complanata)* is consistently supported by the three trees (Anatomy, Alleles, and Wagner-1) which contain both species. Its grouping with *T. burchi,* evident in the Anatomy and Alleles Trees (combined weight = 1.3), is strongly contradicted by the Wagner-1 Tree (weight = 1.0), in which *burchi* appears between *Webbhelix* and the *Neohelix-Xolotrema* lineage. Dissections of *T. burchi* were reexamined, but no evidence was found for reinterpreting it anatomically; therefore in the Consensus Tree (Fig. 28) *burchi* is retained next to the *tennesseensis* group with a question mark denoting its problematic status. The position of the *tennesseensis* group-?*burchi* lineage as sister group to the *vulgata* group *platysayoides* lineage is clear-cut on both the Anatomy and Wagner-1 Trees (combined weight = 2.0) and is only mildly contradicted by the grouping of *tennesseensis* with *tridentata* and *juxtidens* in the Wagner-2 Tree (weight = 0.4).

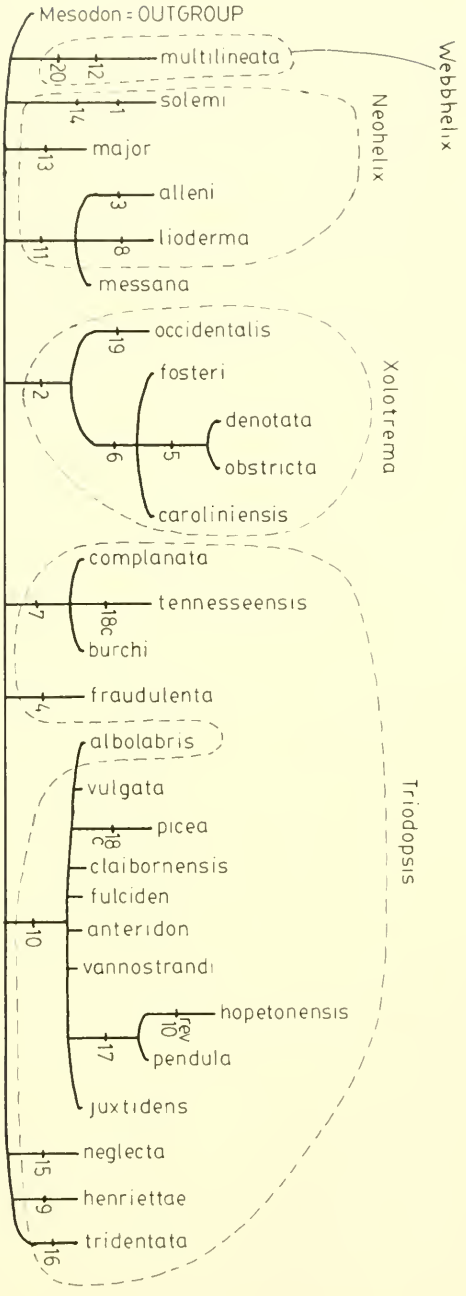

FIG. 25. "Alleles Tree": a phylogenetic hypothesis for the eastern American triodopsines based on allozymes, with *Mesodon* as outgroup. The 20 uniquely derived alleles are listed in Table 3. This tree is the consensus of 50 trees of equal and maximum parsimony generated by PAUP, with a consistency index of .950.

The phylogeny of the remainder of *Triodopsis* is fairly consistent among the four trees, and generally supports the Anatomy Tree (Fig. 24). The *tridentata* group *(tridentata, anteridon, fallax, obsoleta, hopetonensis, palustris, messana, alabamensis,*

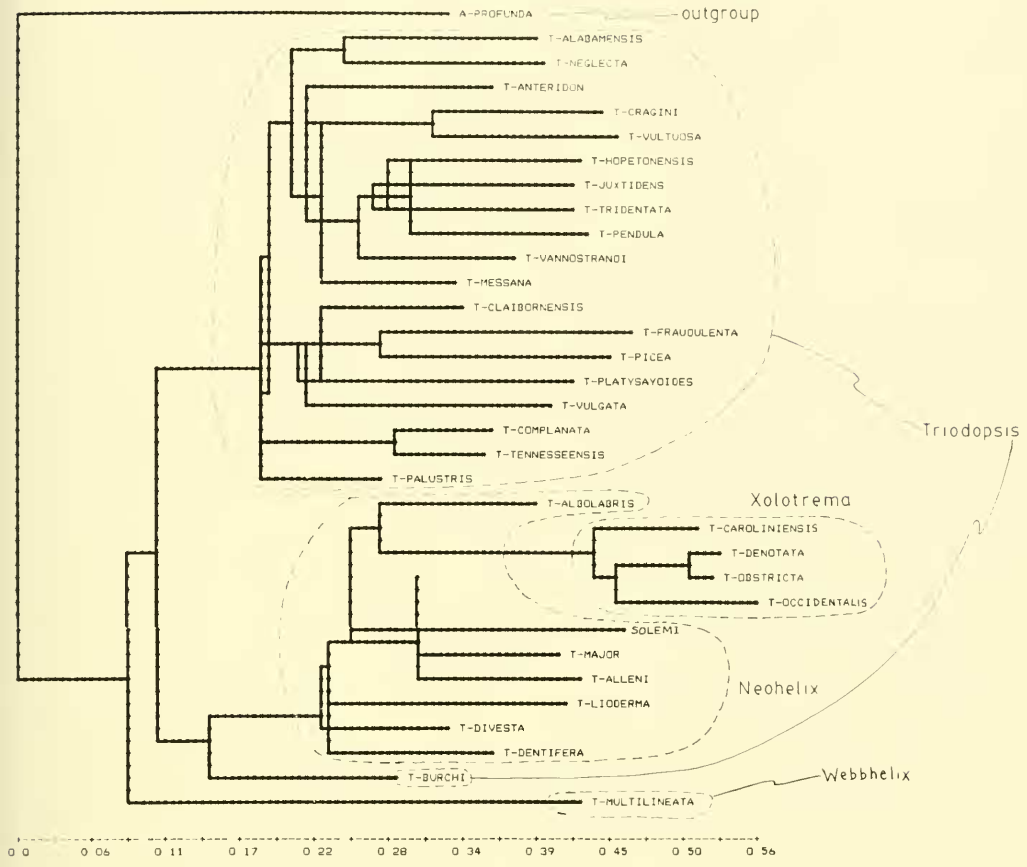

FIG. 26. "Wagner-1 Tree": a distance-Wagner tree for 32 species of eastern American triodopsines, with *Allogona* as outgroup. Computed from the Prevosti distance matrix based on 16 allozymic loci (Table 2, upper half). The cophenetic correlation is .897. The branch lengths are optimized.

vannostrandi, and *soelneri)* and the *juxtidens* group *(juxtidens, discoidea, pendula,* and *neglecta)* cannot be distinguished electrophoretically (Figs. 25–27); nevertheless their separation is accepted on both anatomical and biogeographic grounds. The differences in pore position and peduncle size between the *tridentata* and *juxtidens* groups, although not extreme and not always easy to detect in dissection, are disjunct (see previous discussions under Transformations 42, 43, 49, and 50). Biogeographically, none of the four species of the *juxtidens* group (0%) show range overlap (Fig. 49), whereas there are approximately 10 range overlaps among the 10 species of the *tridentata* group (10/ (10 take 2) = 10/45 = 22%); this is consistent with the view that the *juxtidens* group is more recently evolved and less differentiated. The lack of electrophoretic differentiation between the *tridentata* and *juxtidens* groups is interpreted as evidence that their split was relatively recent.

The *T. cragini* group *(cragini, vultuosa,* and *henriettae)* is tightly coherent in both the Anatomy and Wagner-1 Trees (Figs. 24, 26), although *henriettae* is missing from the latter. In the Wagner-2 Tree (Fig. 27), *henriettae* and two populations of *vultuosa* cluster closely, with *cragini* more distantly connected and with *fulciden* intervening, which is discussed below. The consensus of these three trees (the Alleles Tree contains no information beyond *henriettae's* possession of the unique, derived allele lcd_{104}) is that the *cragini* group is well defined and that *cragini* is

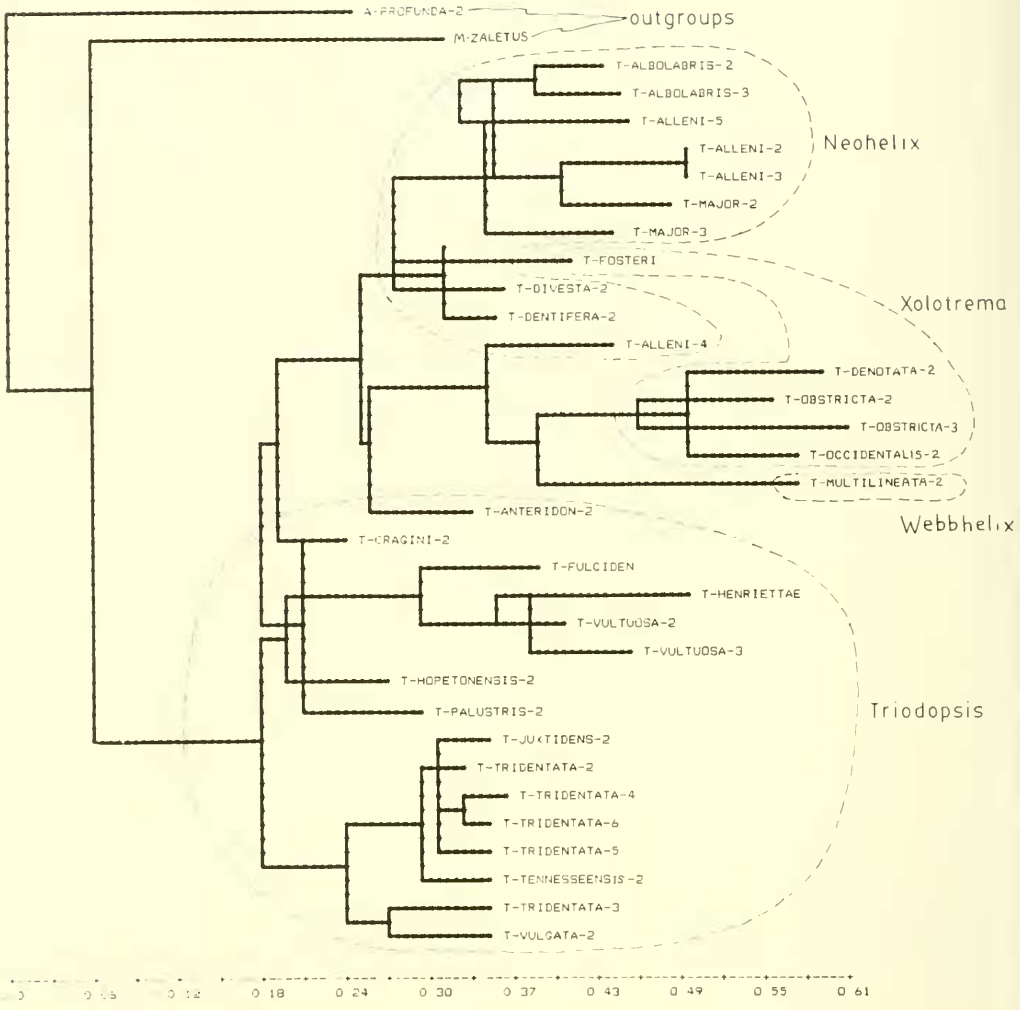

FIG. 27. "Wagner-2 Tree": a distance-Wagner tree for 3 additional species and 29 additional populations of 18 of the species of eastern American triodopsines represented in the Wagner-1 Tree (Fig. 26), with *Allogona profunda* and *Mesodon zaletus* as outgroups. Computed from the Prevosti distance matrix based on the 8 allozymic loci for which all populations had complete data (Table 2, lower half). The cophenetic correlation is .883; the branch lengths are optimized.

probably the most plesiomorphous species of the group. The position of the *cragini* group is outside the *tridentata-juxtidens* lineage in the Anatomy Tree (weight 1.0), shallowly within this lineage in the Wagner-1 Tree (weight 1.0), and outside this lineage in the Wagner-2 Tree (weight 0.4). The consensus, therefore, is the separation of these lineages as sister groups.

Complete electrophoretic data were lacking for *T. fulciden,* and none were available for *T. rugosa,* so the only test of their paired position in the Anatomy Tree (in which *rugosa* equals the "*fraudulenta* group"), is *fulciden's* position in the Wagner-2 Tree. Its close relationship to the *cragini* group in this tree in entirely supportive of its being a sister group to the *cragini-tridentata-juxtidens* lineage (Fig. 24), but could also denote its being a sister group of the *cragini* group alone. In the Consensus Tree (Fig. 28), therefore, the *fulciden-rugosa* pair (named the *rugosa* group) is positioned as in the Anatomy Tree (Fig. 24), but with a question mark. Since data for *rugosa* are

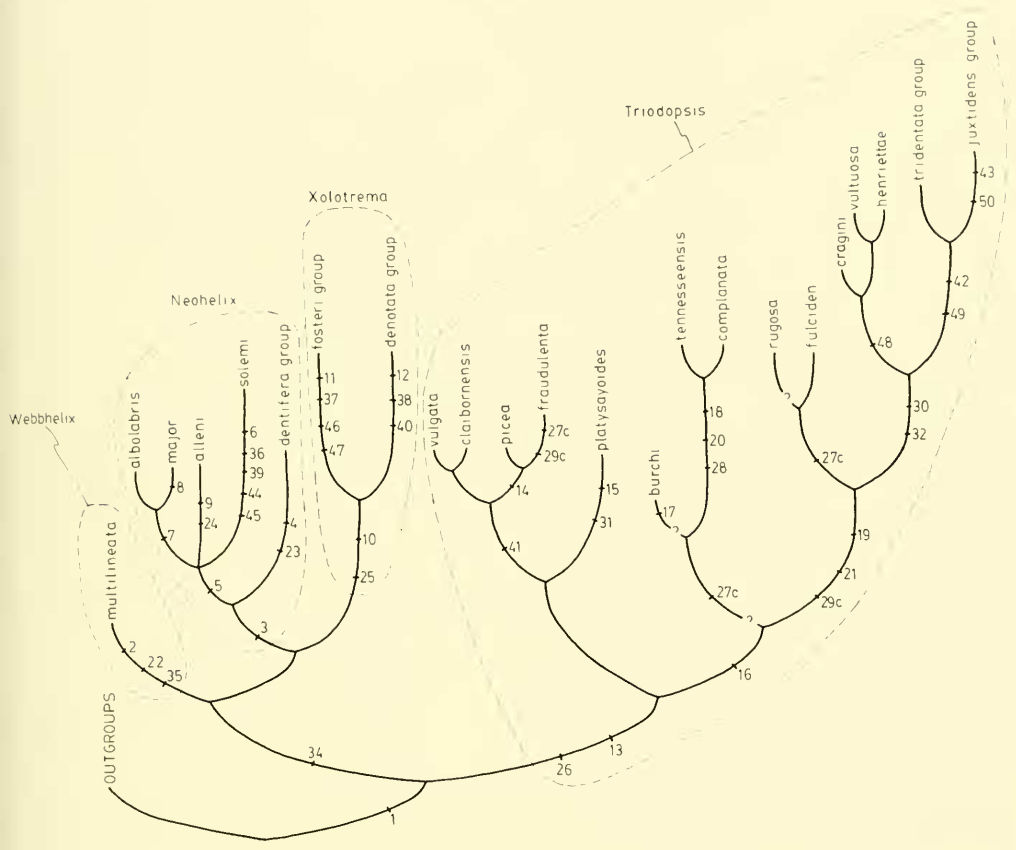

FIG. 28. "Consensus Tree": the robust phylogenetic hypothesis for the eastern triodopsines, representing the weighted consensus of the Anatomy, Alleles, Wagner-1, and Wagner-2 Trees (Figs. 24–27).

scant, this pairing is also uncertain, so *rugosa's* position in is also marked with a question mark.

The completed Consensus Tree for the eastern American triodopsines is presented in Fig. 28, labeled with the suggested anatomical charcter-state transformations as reassessed in the light of electrophoretic evidence. The Consensus Tree carries two convergences in transformation 27 and a single convergence in transformation 29. It represents a robust consensus between electrophoretic and anatomical data.

CONCHOLOGICAL VARIATION

Conchological illustrations of eastern American triodopsine species are presented in Figs. 29–45. Also included for comparative purposes is an illustration of *Allogona profunda*, the only eastern ashmunelline (Fig. 46a–b). Shell variation of eastern triodopsines has been thoroughly discussed by Pilsbry (1940), Vagvolgyi (1968), and Grimm (1975). An illustrated key to most of the species is contained in Burch (1962). It is important to remember when identifying any eastern American triodopsine that many species of the polygyrine genus *Mesodon* have closely convergent shells.

REVISION OF THE *NEOHELIX ALBOLABRIS* GROUP

The following classification is proposed, based on analyses of penis and shell. The complete systematic review is presented in Appendix B.

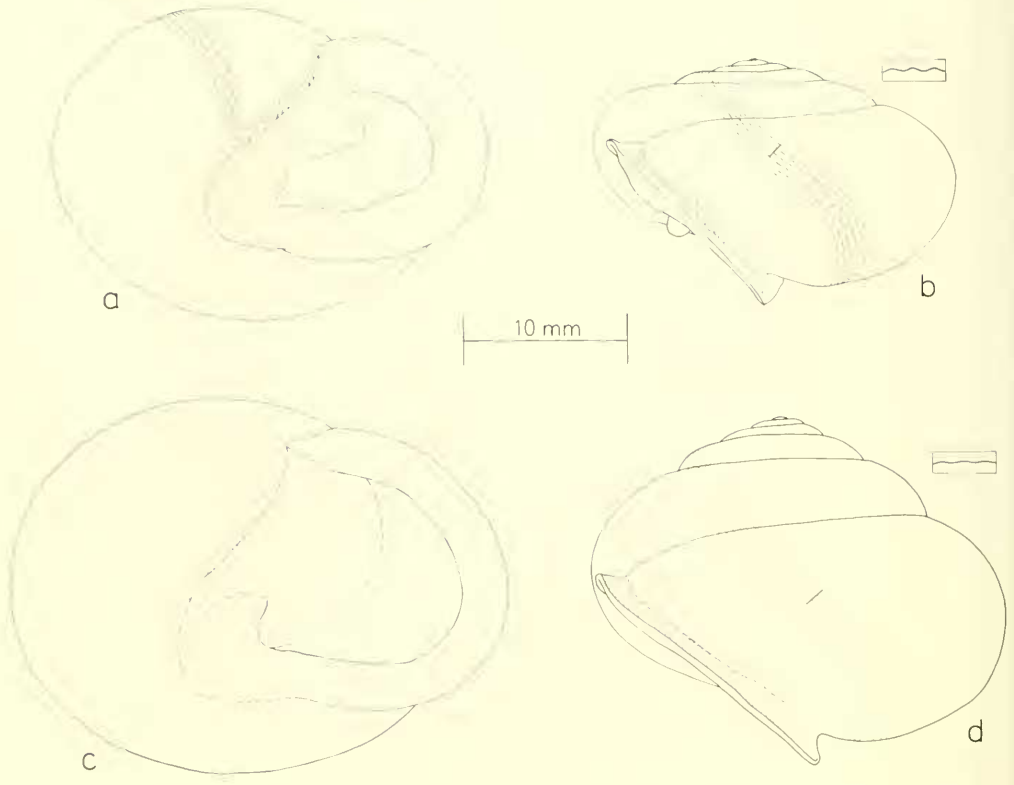

FIG. 29. Shells. **a–b.** *Neohelix dentifera* (Binney, 1837). FMNH 214810 #8. **c–d.** *Neohelix albolabris albolabris* (Say, 1816). FMNH 214920 #14.

albolabris group
albolabris
albolabris albolabris (Say, 1816)
albolabris bogani Emberton, new subspecies
major (Binney, 1837)
alleni group
alleni
alleni alleni (Sampson, 1883)
alleni fuscolabris (Pilsbry, 1903)
solemi Emberton, new species

Genitalic analysis

Species identification of each of the 46 populations (Fig. 47) was made by comparing its penial morphology with Figs. 2d, 3, 4, and 6b. Differences among *albolabris, alleni, major*, and *solemi* in upper penial sculpture were extremely stable over their geographical ranges, which made identifications easy and straightforward. For 39 of the populations, penial sculpture was examined by dissecting one to three specimens per population; for two populations (numbers 5, 32), specimens had partially everted their penes in the drowning jar, so could be identified without dissection; the remaining 5 populations (numbers 16–19, 27) were identified from published anatomical illustrations (Simpson, 1901; Pilsbry, 1940; Webb, 1952, 1954a).

The results of the penial-morphological measurements are presented in Table 4 as ranges over the three measured populations (one specimen per population). For each of the 7 variables, value ranges are underlined which do no overlap the value range of *albolabris albolabris*. Because of the small sample sizes and non-normal distributions, these differences were not tested for statistical significance. Between the two subspecies of *albolabris* there was no difference detected in any of the 7 penial-morphological variables, therefore they were pooled for cladistic analysis.

From Table 4, seven new penial-morphological transformations (transformations A–G) are proposed for a cladistic analysis of *albolabris, alleni, major,* and *solemi,* using

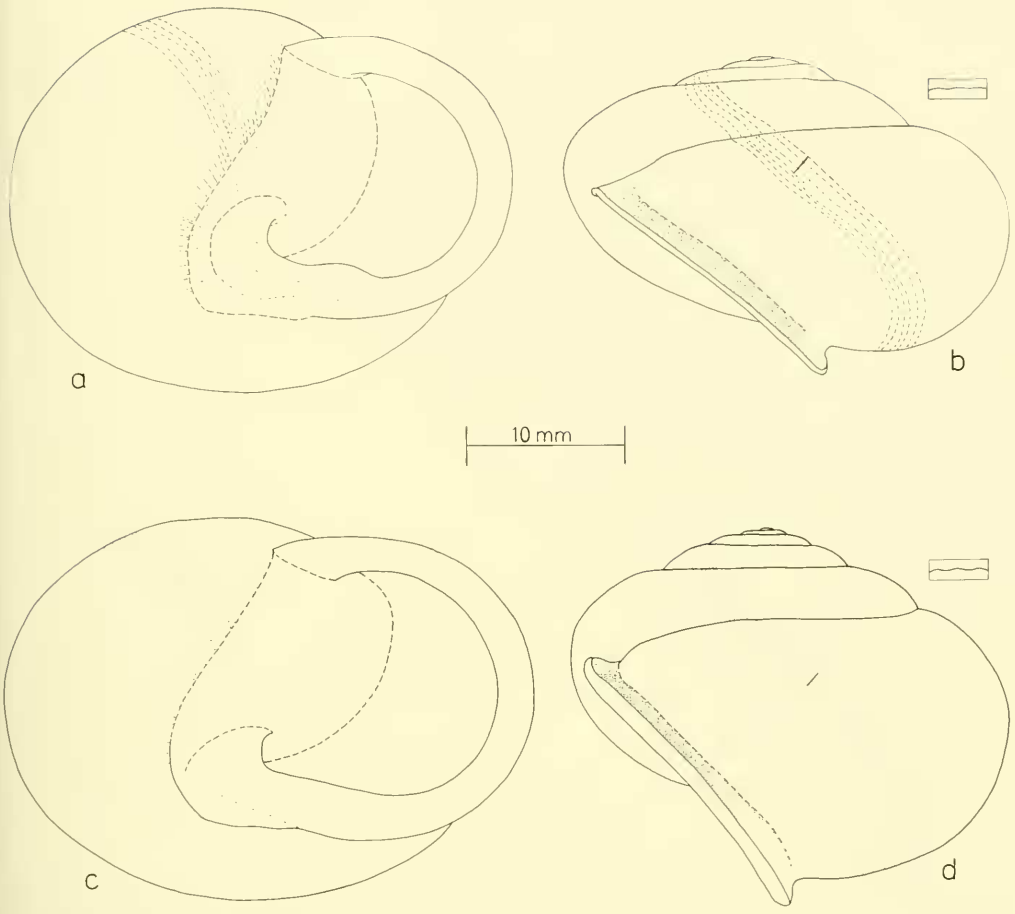

FIG. 30. Shells. **a–b.** *Neohelix alleni alleni* (Sampson, 1883). FMNH 214913 #B. **c–d.** *Neohelix major* (Binney, 1837). FMNH 214933 #H.

Webbhelix and the *dentifera* group as outgroups (Fig. 28). The format used is the same as used previously for transformations 1–50.

Transformation A—Preceding transformations: none.

Plesiomorphous state: penis, pilastral lappets, and wall pustules all moderate in size: penis length variable with median ca 13–14 mm, pilastral lappets less than .3 mm high, wall pustules less than .15 mm wide. Present in (outgroups): *Webbhelix multilineata* (penis and pustules), *N. dentifera* group (penis, lappets, upper pustules), *albolabris, alleni, solemi* (penis, lappets, basolateral pustules).

Apomorphous state: penis, pilastral lappets, and wall pustules all large: penis length invariable at 17 mm, pilastral lappets higher than .5 mm, wall pustules wider than .16 mm. Formerly and now present in: *major*.

Discussion. The penis of *major* (Fig. 4a) looks much like a hypertrophied version of *albolabris's* (Fig. 2d), so it appears that its longer penis and larger pilastral lappets and wall pustules are intercorrelated features of a general enlargement. Of the outgroups, all have a moderate penis length. Only *albolabris* (Fig. 2d), *alleni* (Fig. 3a, c), and *solemi* (Fig. 6b) have the plesiomorphous lappet height, since *Webbhelix multilineata* (Fig. 6a) lacks lappets and the *dentifera* group (Figs. 2a, 5a, d) has them doubled (Transformation 4). The plesiomorphous wall pustule size is unmodified only in *W. multilineata* (Fig. 6a), *albolabris* (Fig. 2d), and *alleni* (Fig. 3a, c); the

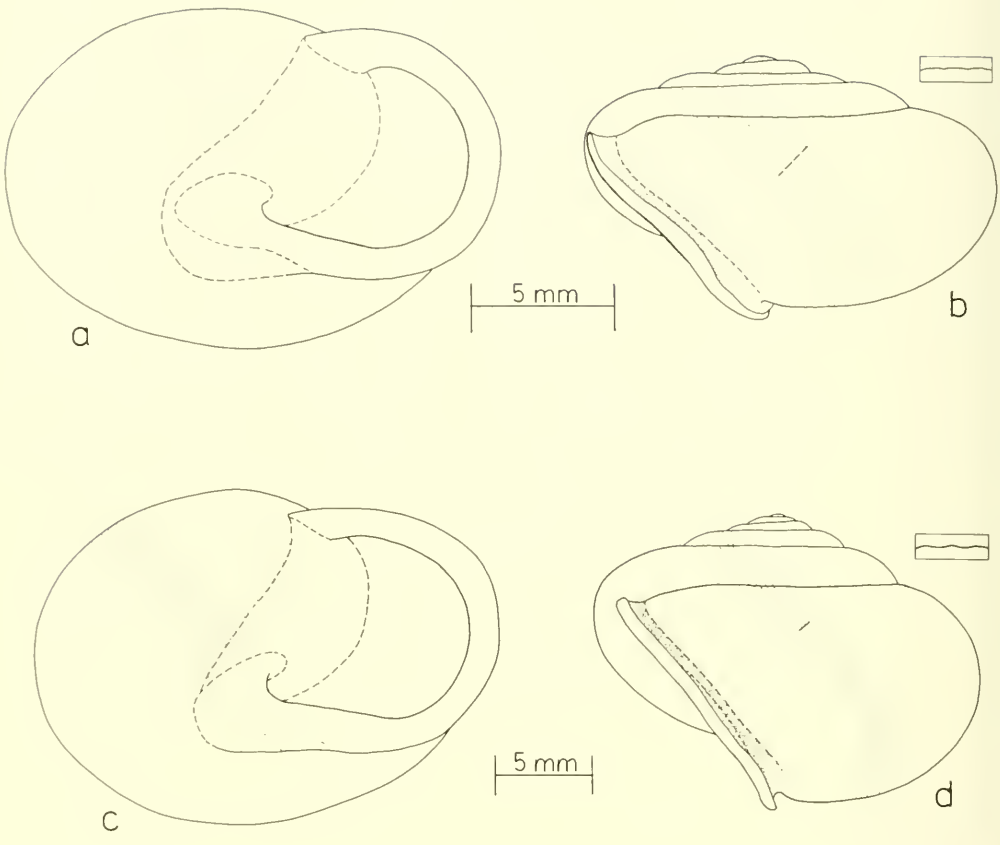

FIG. 31. Shells. **a–b.** *Neohelix lioderma* (Pilsbry, 1902). FMNH 214844 #A. **c–d.** *Neohelix divesta* (Gould, 1848). FMNH 214813 #A.

wall pustules are enlarged basally (Transformation 23) in the *dentifera* group (Figs. 2a, 5a, d) and enlarged everywhere but baso-laterally (Transformation B, below) in *solemi* (Fig. 6b).

Transformation B—Preceding transformations: none.

Plesiomorphous state: all wall pustules moderate and approximately equal in size, less than 0.15 mm wide. Present in (outgroups): *W. multilineata* (Fig. 6a), *albolabris* (Fig. 2d), *alleni* (Fig. 3a, c).

Apomorphous state: all but the baso-lateral wall pustules large, wider than .20 mm. Formerly and now present in *solemi* (Fig. 6b).

Discussion. Large wall pustules, 5–6 per 1.3 mm, occur in both *major* and *solemi* (Table 4, column 3), but this appears to be due to convergence. The large wall pustules of *solemi* (Fig. 6b) are neither uniformly sized nor accompanied by a large penis and large pilastral lappets, as they are in *major* (Fig. 4a).

Transformation C—Preceding transformations: none.

Plesiomorphous state: pilastral lappets about as wide as the wall pustules. Present in (outgroup): *alleni* (Fig. 3a, c), *solemi* (unmodified baso-lateral wall pustules: Fig. 6b).

Apomorphous state: pilastral lappets approximately twice as wide as the wall pustules. Formerly and now present in: *albolabris* (Fig. 2d), *major* (Fig. 4a).

Discussion. According to Table 4 (third and fourth columns), the pilastral lappets are slightly less dense than the columns of wall pustules in *alleni* (15–18 vs. 18–22 per 2.6 mm), and slightly more dense than the enlarged, central columns of wall pustules in *solemi* (14–15 vs. 8–12 per 2.6 mm). In contrast, the pilastral lappets in *albolabris* are

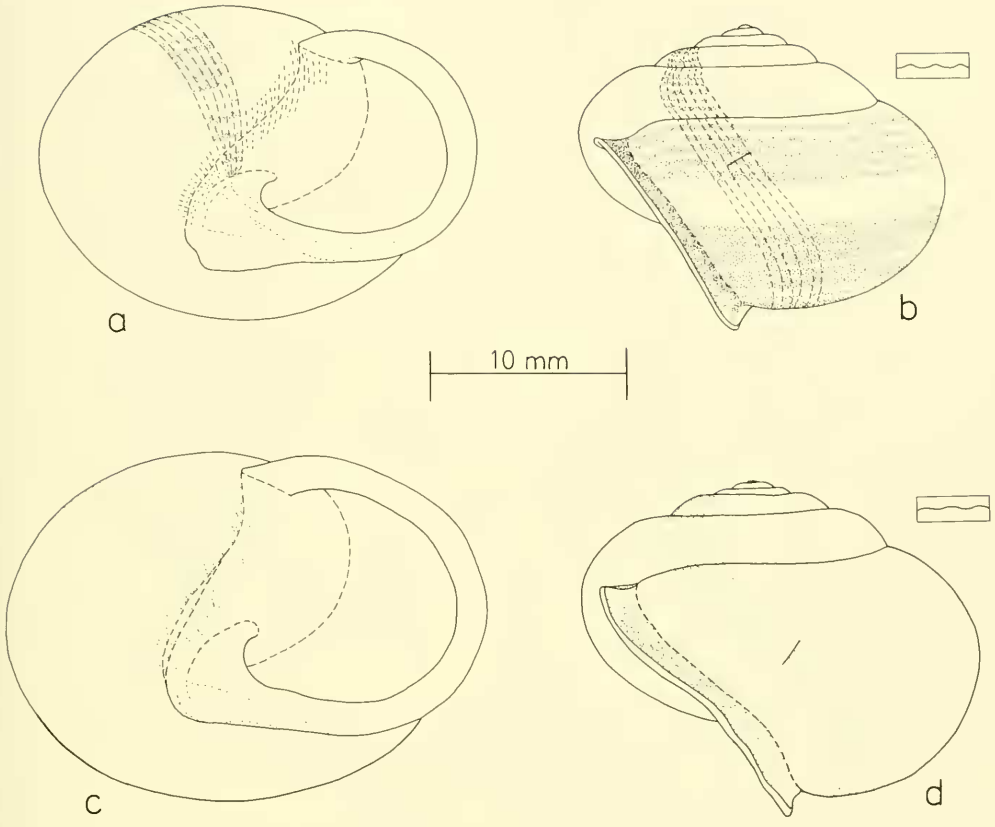

FIG. 32. Shells. **a–b.** *Webbhelix multilineata* (Say, 1821). FMNH 214848 #2. **c–d.** *Neohelix solemi* Emberton, new species. FMNH 214936 #1.

about twice as dense as the columns of wall pustules (8–11 vs. 16–24 for *albolabris albolabris,* and 9–14 vs. 20–22 for *albolabris bogani*), and the same is true of *major* (4–5 vs. 10–16 per 2.6 mm). Since pilastral lappets seem to be derived from wall pustules by lateral fusion (see discussion under Transformation 5), it is assumed that the equal density, or equal width, seen in *alleni* and *solemi* is plesiomorphous. Close examination of Figs. 2d and 11a reveals evidence that the double-sized lappets of *albolabris* and *major* resulted from vertical fusion: one of *albolabris's* lappets has a lateral groove, and two of *major's* lappets have pieces of lappets angled beneath them laterally. This rather obvious character-state transformation was overlooked in the previous analysis.

Transformation D—Preceding transformations: none.

Plesiomorphous state: verge large, greater than .12 the penial length. Present in (outgroups): *W. multilineata* (Fig. 6a), *dentifera* group (Figs. 2a, 5a, d), *albolabris* (Fig. 2d), *major* (Fig. 4a).

Apomorphous state: verge moderate in size, less than .09 the penial length. Formerly and now present in: *alleni* (Fig. 3a, c).

Discussion. The unique, small verge of *solemi,* which is only .01–.05 the penial length (Table 11, column 4) was already used as Transformation 36 (Type 1 small verge). As discussed under that Transformation, the moderately sized terminal verge of *alleni* is not homologous with that of *solemi;* instead, it is structurally (Fig. 3b) very similar to the

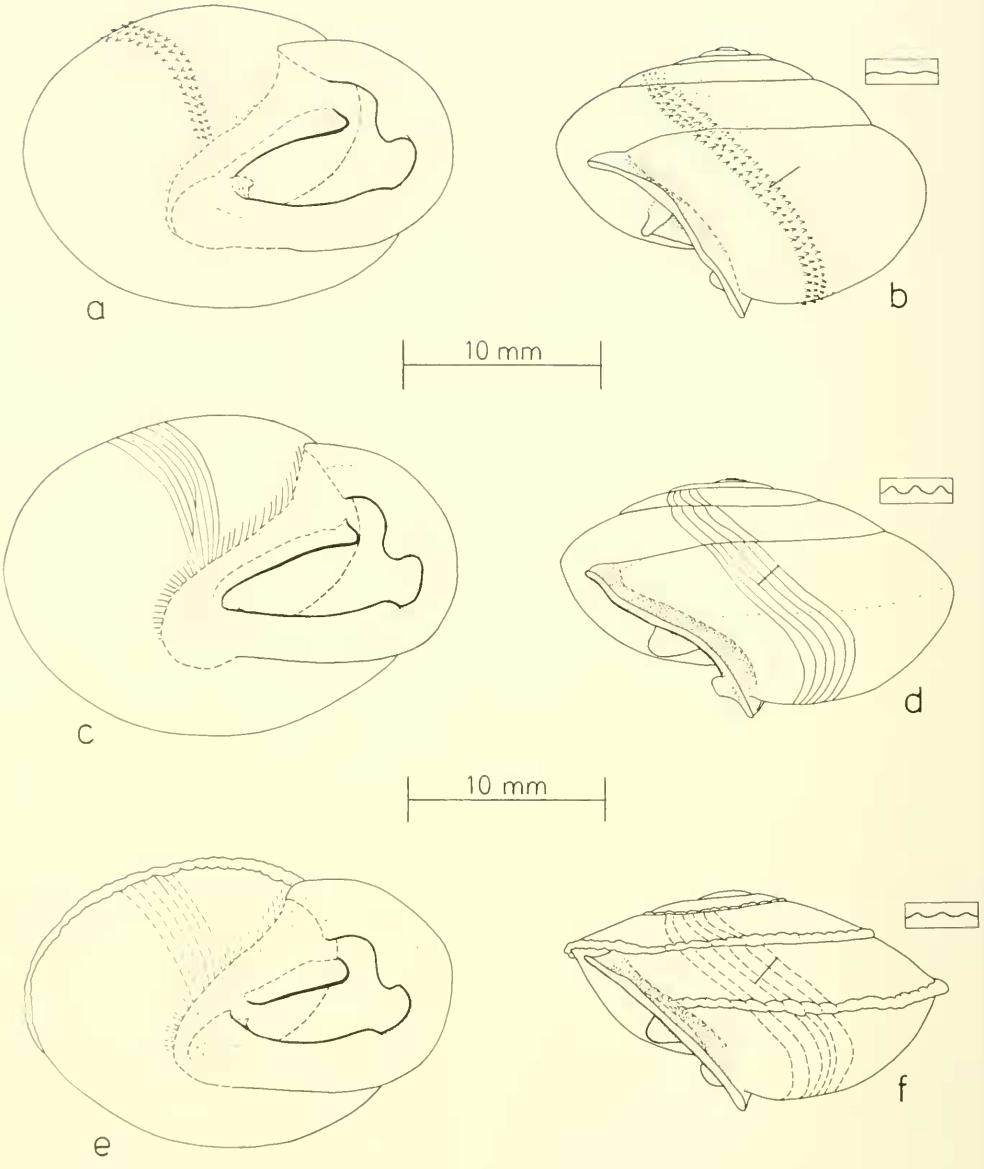

FIG. 33. Shells. **a–b.** *Xolotrema denotata* (Férussac, 1821). FMNH 214806 #1. **c–d.** *Xolotrema caroliniensis* (Lea, 1834). FMNH 171142 #B. **e–f.** *Xolotrema obstricta* (Say, 1821). FMNH 214852 #1.

verges of *albolabris* (Fig. 2f), *major* (Fig. 4b), and *divesta* (Fig. 5e), which differ from it only in their larger size.

Transformation E—Preceding transformations: none.

Plesiomorphous state: pilaster moderate in breadth, .06–.12 the penial length. Present in (outgroups): *W. multilineata* (Fig. 6a), *dentifera* group (Figs. 2a, 5a, d), *albolabris* (Fig. 2d), *major* (Fig. 4a), *alleni* (Fig. 3a, c).

Apomorphous state: pilaster narrow, .02–.04 the penial length. Formerly and now present in: *solemi* (Fig. 6b).

Discussion. The uniquely narrow dorsal pilaster of *solemi* (table 4, column 5) probably

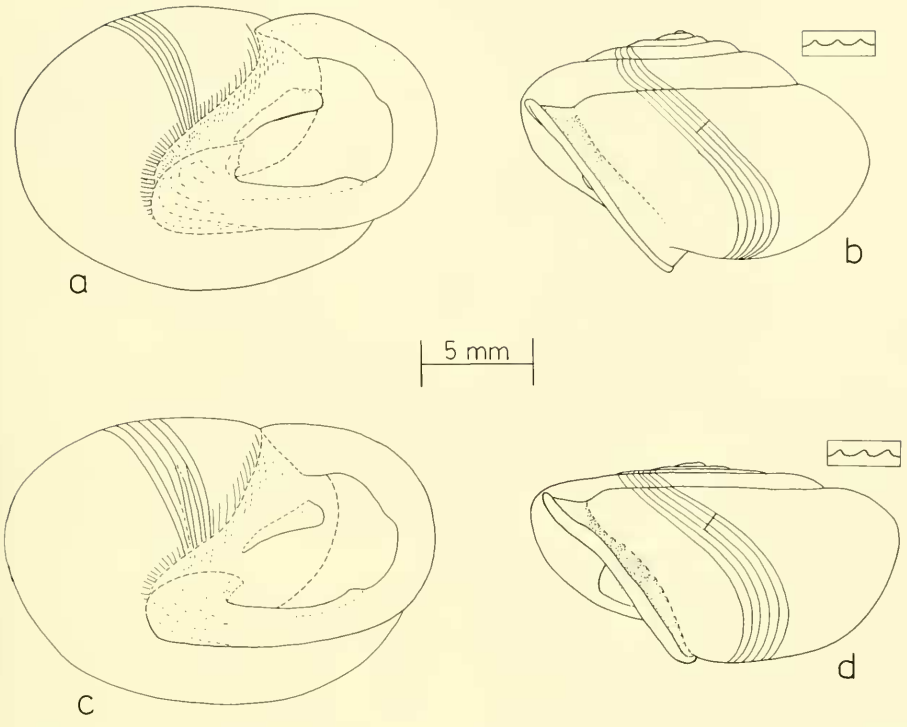

FIG. 34. Shells. **a–b.** *Xolotrema fosteri* (F. C. Baker, 1932). FMNH 214817 #15. **c–d.** *Xolotrema occidentalis* (Pilsbry & Ferriss, 1907). FMNH 214856 #5.

indicates that it is vestigial. The indistinct lappets on this dorsal pilaster (Transformation 6) and the apparently compensatory ventral pilaster (Transformation 44) support this view. It seems likely that when *solemi* evolved a (dorsally) subterminal pore (Transformation 39), the adaptive significance of which is hypothesized in Appendix A, both its verge (Transformation 36) and its dorsal pilaster (Transformation E) were no longer functional and so became vestigial.

Transformation F—Preceding transformations: none.

Plesiomorphous state: retractor muscle's origin distant from the penial apex, .4–.7 the penial length along the vas deferens. Present in (outgroups): *W. multilineata* (Binney, 1851, pl. 8, fig. 2), *dentifera* (Pilsbry, 1940, fig. 491), *divesta* (Pilsbry, 1940, fig. 492; Solem, 1976, fig. 4), *albolabris,* and *major* (Table 4, column 6).

Apomorphous state: retractor muscle's origin close to the penial apex, .1–.3 the penial length along the vas deferens. Formerly and now present in: *alleni, solemi* (Table 4, column 6).

Discussion. In the absence of detailed differences suggesting convergence, it is suggested that this apomorphous character state is homologous in *alleni* and *solemi.*

Transformation G—Preceding transformations: none.

Plesiomorphous state: vas deferens long, over 4 times as long as the penis. Present in (outgroups): *dentifera* (Pilsbry, 1940, fig. 491), (Pilsbry, 1940, fig. 492), *albolabris* (e.g. Pilsbry, 1940, fig. 488) (Table 4, last column), *major* (Table 4, last column).

Apomorphous state: vas deferens short, about 2 times as long as the penis. Formerly and now present in: *alleni, solemi* (Table 4, last column).

Discussion. This hypothesized transformation is somewhat problematic. A short vas deferens occurs in *multilineata* (Binney, 1851, pl. 8, fig. 2), in some *divesta* (Solem, 1976, fig. 4a), and in juvenile *albolabris* (Webb, 1954a, pl. 7, fig. 29); which suggests that the

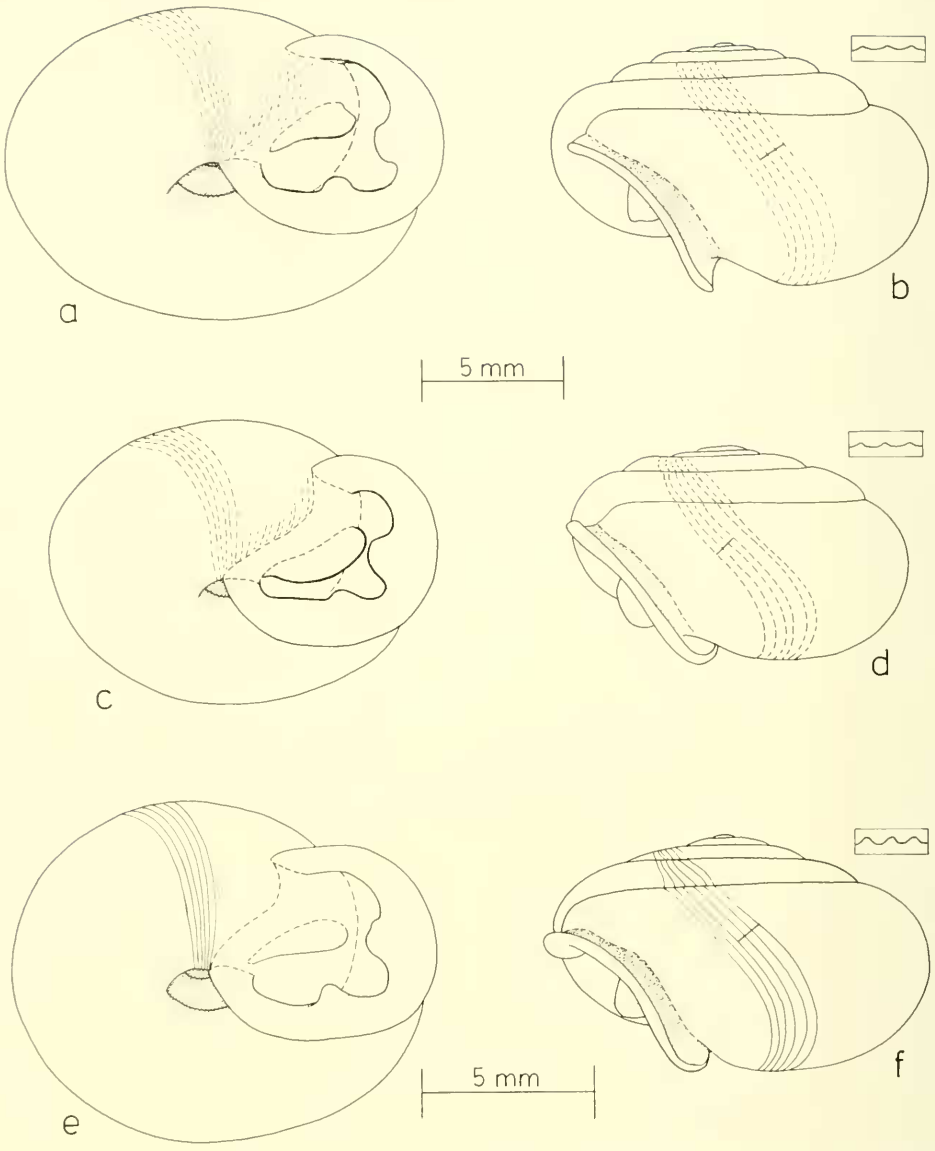

FIG. 35. Shells. **a–b.** *Triodopsis vulgata* Pilsbry, 1940. FMNH 214884 #A. **c–d.** *Triodopsis picea* Hubricht, 1958. FMNH 214860 #15. **e–f.** *Triodopsis claibornensis* Lutz, 1950. FMNH 214800 #A.

long vas deferens of *dentifera, divesta, albolabris,* and *major* may be apomorphous rather than plesiomorphous. However, in keeping with the hypothesis that the *dentifera* group is the immediate outgroup of the *albolabris* group (Fig. 28), outgroup comparison dictates that the short vas deferens of *alleni* and *solemi* is apomorphous. For lack of evidence to the contrary, it is assumed homologous in these two species.

Cladistic analysis

With the addition of Transformations A–G to those used in the Anatomy Tree (Transformations 5–9, 24, 36, 39, 44, 45), there were a total 17 penial-morphological transformations with which to construct a cladogram. These yielded a single, parsimonious cladogram, free of convergence and reversal, which is illustrated in Fig. 48. The only change this

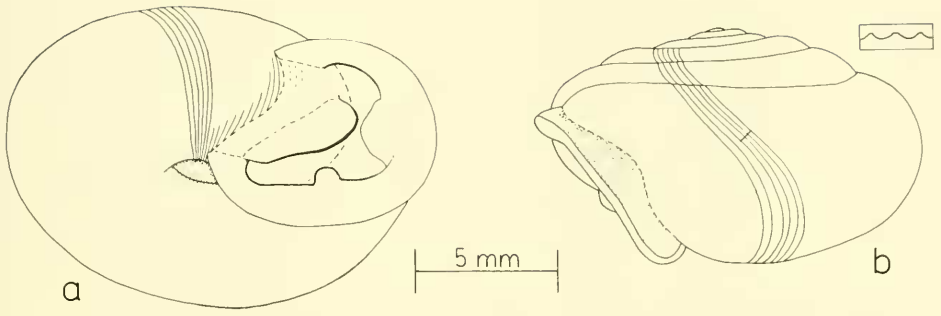

FIG. 36. Shell. **a–b.** *Triodopsis fraudulenta* (Pilsbry, 1894). FMNH 214822 #A.

represents from the Consensus Tree (Fig. 28) is in grouping *alleni* and *solemi* in a monophyletic lineage, designated the *alleni* group.

Shell analysis

The complete shell measurements are presented in Table 6, and are referred to in the systematic review of the *albolabris* and *alleni* groups (Appendix B). The 8 conchological variables, when calculated from the raw measurements (Table 6) by the methods described in Table 5, and when standardized and subjected to discriminant analysis, yielded a discriminant function (Table 7) which correctly classified to subspecies or species 44, or 94%, of the 47 analyzed shells.

The three misclassified shells are marked by asterisks in Table 6. One shell of *alleni alleni* (population 3, specimen #8) was misclassified as *alleni fuscolabris,* with a posterior probability of membership in that subspecies of .66; its probability of correct classification was .34. Two shells of *albolabris albolabris* (population 11, specimen #4; and population 12, specimen #17) were misclassified as *solemi,* with posterior probabilities of membership in that species of .60 and .53 respectively; their probabilities of correct classification were .24 and .47, with the former specimen also having a .16 probability of misclassification in *albolabris bogani.*

Thus, overall, the discriminant function (Table 7) was quite successful in differentiating the 6 taxa by the 8 shell variables (Table 5). The fact that 8 of the 9 total shells of *alleni* were correctly classified to subspecies, and that the ninth shell had a .34 probability of correct classification, is persuasive evidence of the conchological differentiation between the western *alleni alleni* and the disjunct eastern *alleni fuscolabris* (Figs. 46, 50). Likewise, the fact that all of the 21 shells of *albolabris* which were correctly classified to species were also correctly classified to subspecies, testifies to the conchological differentiation between the eastern *albolabris albolabris* and the western *albolabris bogani* (Figs. 47, 49). The discriminant function's marginal failure to differentiate two shells of *albolabris albolabris* from *solemi* points out the necessity of dissection for reliably identifying *albolabris-alleni*-group snails along the northern Piedmont and Coastal Plain (Figs. 47).

Revised classification

The systematic review of the *albolabris* and *alleni* groups is presented in Appendix B. In it, extensive use was made of the tabulated discriminant function (Table 7). Because all 8 variables were standardized (to mean = 0, standard deviation = 1), they received equal weight in the analysis. Therefore, in the discriminant function (Table 7), the total range of a variable is an indication of its value in taxonomically discriminating among the shells. Thus, for example, GLOSSY's range from −10.1 to 8.0 indicates that it is a more powerful discriminator than RELSPIRE, with its smaller range of −1.7 to 1.5. This discriminant function is biased to some degree by the included taxa and the included shells, such that, for example, a reanalysis comparing only *albolabris albolabris* and *albolabris bogani* would produce a different discriminant function emphasizing different variables. In short, Table 7 is not the final or the best word on how to tell these taxa apart by shell characters; it is better viewed as an interim guideline.

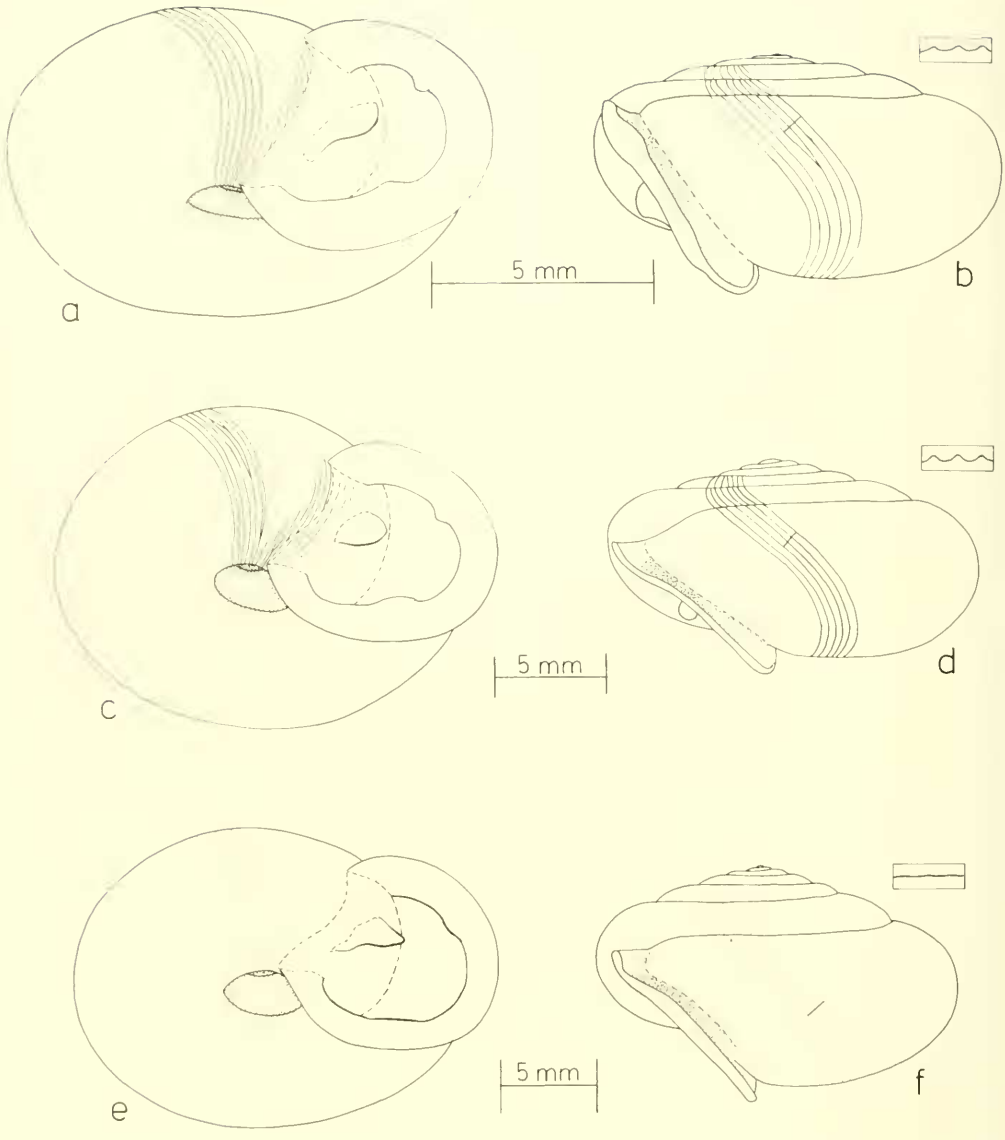

FIG. 37. Shells. **a–b.** *Triodopsis burchi* Hubricht, 1950. FMNH 214797 #10. **c–d.** *Triodopsis tennesseensis* (Walker & Pilsbry, 1902). FMNH 214864 #7. **e–f.** *Triodopsis complanata* (Pilsbry, 1898). Hubricht 17932 #A.

GENERAL SUPRASPECIFIC REVISION

The supraspecific revision of the eastern triodopsines based on the consensus phylogeny (Fig. 28) is listed below and is presented in detail in Appendix C. This revision groups the 40 species into 4 genera, 14 species groups, and 8 species subgroups. Most of the species groups are the same as those temporarily introduced in Table 1 and used throughout the Anatomical and the electrophoretic Trees (Figs. 24–27). Changes from Table 1 are establishment of the *albolabris* and *alleni* groups, expansion of the *vulgata* group to include *fraudulenta* and *picea,* deletion of the *fraudulenta* group, and creation of the *rugosa* group *(rugosa* and *fulciden).* The decision was made reluctantly to submerge

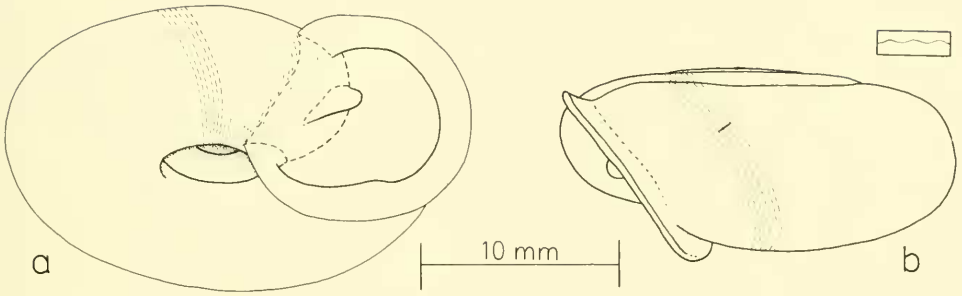

FIG. 38. Shell. **a–b.** *Triodopsis platysayoides* (Brooks, 1933). FMNH 214861 #2.

Webb's subgenera *Wilcoxorbis* Webb, 1952 (= the *fosteri* group) and *Haroldorbis* Webb, 1959 (= the *cragini* group), and section *Shelfordorbis* Webb, 1959 (= the *vulgata* group), because retaining them would have required coining 11 additional subgenera in order to keep the taxonomy hierarchically consistent. The genera and species groups are arranged alphabetically here; in Appendix C they are arranged phylogenetically.

Neohelix von Ihering, 1892
  albolabris group
    albolabris (Say, 1816)
    major (Binney, 1837)
  alleni group
    alleni (Sampson, 1883)
    solemi Emberton, new species
  dentifera group
    dentifera subgroup
      dentifera (Binney, 1837)
    divesta subgroup
      divesta (Gould, 1848)
      lioderma (Pilsbry, 1902)
Triodopsis
  burchi group
    burchi Hubricht, 1950
  cragini group
    cragini Call, 1886
    henriettae (Mazÿck, 1877)
    vultuosa (Gould, 1848)
  fallax group
    alabamensis subgroup
      alabamensis (Pilsbry, 1902)
      hopetonensis (Shuttleworth, 1852)
      vannostrandi (Bland, 1875)
    fallax subgroup
      fallax (Say, 1825)
      messana Hubricht, 1952
      obsoleta (Pilsbry, 1894)
      palustris Hubricht, 1958
      soelneri (Henderson, 1907)
  juxtidens group
    juxtidens subgroup
      discoidea (Pilsbry, 1904)
      juxtidens (Pilsbry, 1894)
    neglecta subgroup
      neglecta (Pilsbry, 1899)
      pendula Hubricht, 1952
  platysayoides group
    platysayoides (Brooks, 1933)
  rugosa group
    fulciden? Hubricht, 1952
    rugosa Brooks & MacMillan, 1940
  tennesseensis group
    complanata (Pilsbry, 1898)
    tennesseensis (Walker & Pilsbry, 1902)
  tridentata group
    anteridon (Pilsbry, 1940)
    tridentata (Say, 1816)
  vulgata group
    fraudulenta subgroup
      fraudulenta (Pilsbry, 1894)
      picea Hubricht, 1958
    vulgata subgroup
      claibornensis Lutz, 1950
      vulgata Pilsbry, 1940
Webbhelix
  multilineata (Say, 1821)
Xolotrema
  denotata group
    denotata (Férussac, 1821)
    caroliniensis (Lea, 1834)
    obstricta (Say, 1821)
  fosteri group
    fosteri (F. C. Baker, 1932)
    occidentalis (Pilsbry & Ferris, 1907)

Table 8 compares this classification with those of Pilsbry (1940) based on shell morphology; Webb (1952, 1954, 1959), based on

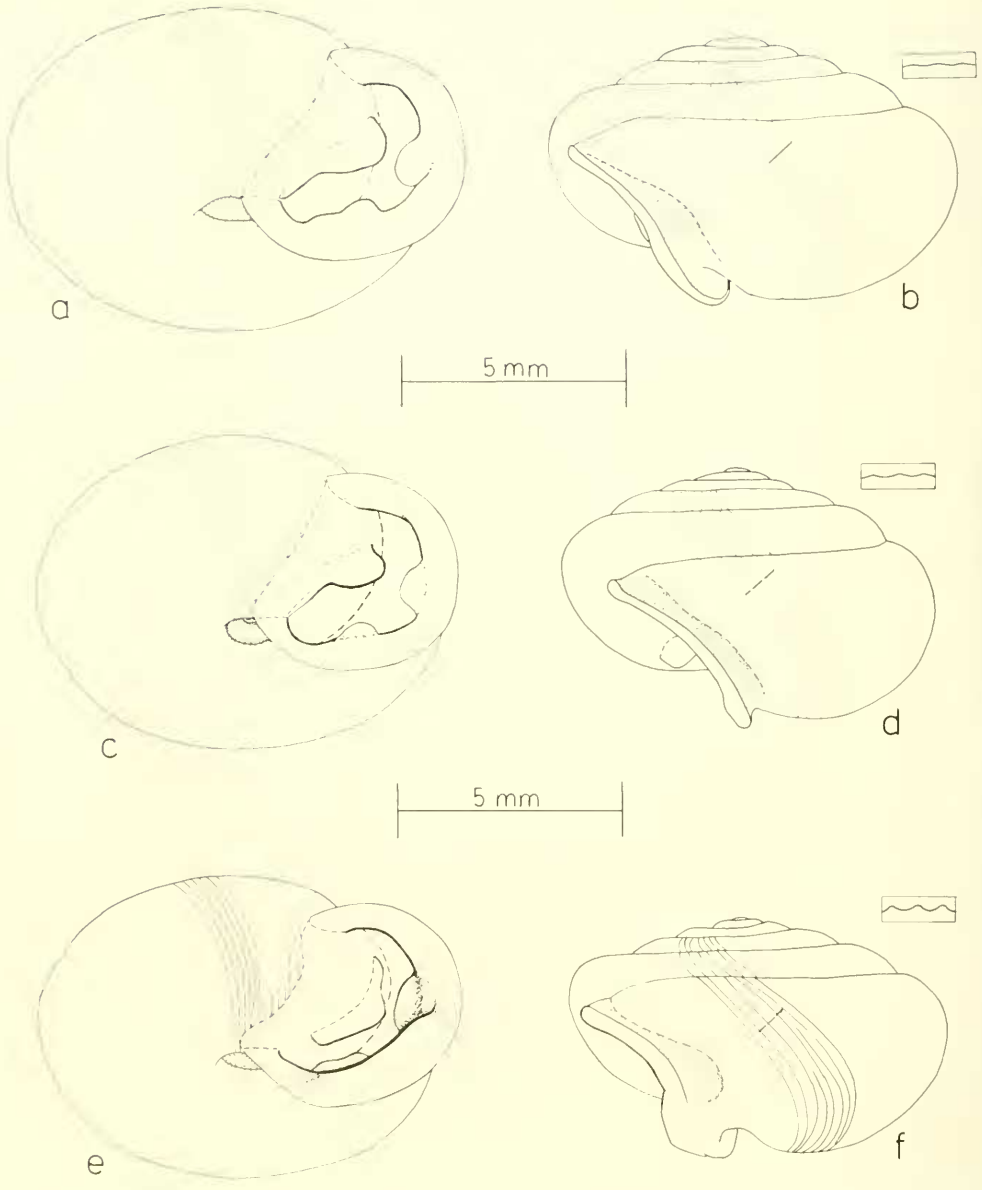

FIG. 39. Shells. **a–b.** *Triodopsis vultuosa* (Gould, 1848). FMNH 214887 #7. **c–d.** *Triodopsis cragini* Call, 1886. FMNH 214803 #2. **e–f.** *Triodopsis henriettae* (Mazÿck, 1877). FMNH 214824 #2.

reproductive anatomy and behavior; and Vagvolgyi (1968), based on shell morphology. Of the 40 species recognized here, Pilsbry classified 33, Webb 15, and Vagvolgyi 38. Irrelevant of the number of species, this revision most closely resembles the classification of Pilsbry (1940) as modified by Hubricht (1985)—the major difference lies in the grouping of species within *Triodopsis* (Table 8).

The systematics of the *Triodopsis fallax* group presented in Appendix C and Table 9 is that of Grimm (1976), as discussed in Appen-

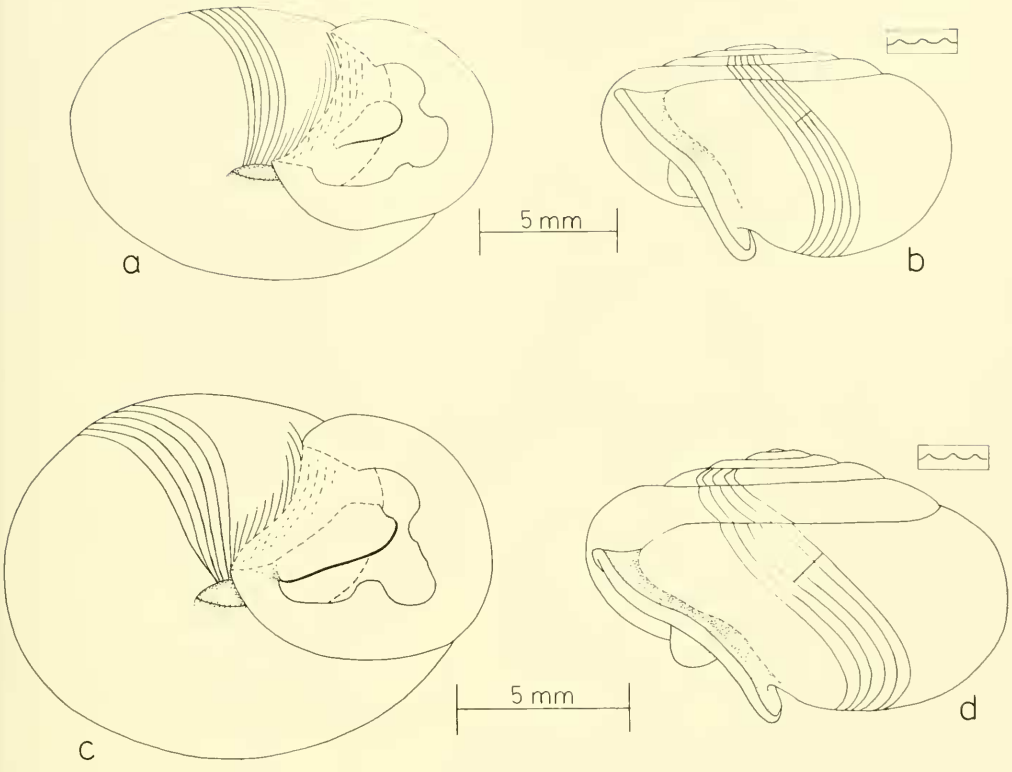

FIG. 40. Shells. **a–b.** *Triodopsis tridentata* (Say, 1816). FMNH 214876 #4. **c–d.** *Triodopsis anteridon* (Pilsbry, 1940). FMNH 214796 #19.

dix D. Division of the *juxtidens* group into *juxtidens* and *neglecta* subgroups is based on shell morphology—see Appendix C.

PATTERNS OF GENITALIC EVOLUTION

The ranges of the 40 species of eastern triodopsines are presented in Fig. 49. These maps were compiled from Hubricht (1985), with corrections for the *Neohelix albolabris* and *alleni* groups.

The maps were used to compare the degree of difference in penial morphology of sister taxa with their geographic range relationship. The results based on 25 comparisons (Table 9) are: sister taxa with virtually identical penes generally have peripatric ranges, those slightly different are generally allopatric, those moderately different are sympatric, but those greatly different are parapatric.

The tests for population-level reproductive character displacement are summarized in Table 10. In none of these 12 tests was there any detectable difference in penial morphology between allopatric and sympatric populations.

PATTERNS OF SHELL EVOLUTION

Fig. 50 shows the phylogenetic pattern of shell morphology among all known living species of eastern North American triodopsines. A general evolutionary pattern is of conchological stasis within genera. In general, each genus is characterized by a distinct shell form: *Neohelix* and *Webbhelix* shells are large, globose, and toothless (Figs. 29–32); *Xolotrema* shells are medium-sized and depressed, with a blade-like parietal tooth and a long basal lamella (Figs. 33, 34); and *Triodopsis* shells are small, subglobose, and tridentate (Figs. 35–45).

Shell convergences among these conchologically distinct genera are rare. *Webbhelix* and *Neohelix* shells are similar appar-

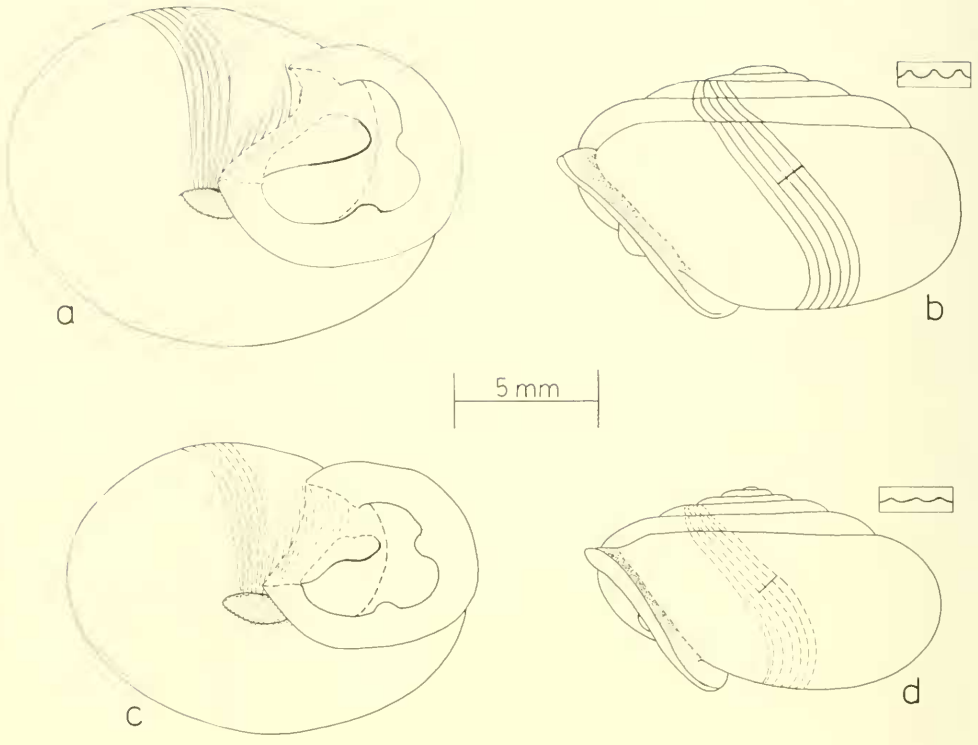

FIG. 41. Shells. **a–b.** *Triodopsis juxtidens* (Pilsbry, 1894). FMNH 214841 #7. **c–d.** *Triodopsis discoidea* (Pilsbry, 1904). FMNH 214811 #A.

ently because they share the plesiomorphous shell morphology seen in some of their outgroups (Fig. 50). One *Neohelix* species—*dentifera* (Fig. 29a–b)—converged slightly on *Xolotrema* by its low spire, strong parietal tooth, and suggestion of a basal lamella. Two lineages of *Triodopsis—platysayoides* (Fig. 38) and *tennesseensis* group (Fig. 37c–f)—converged, apparently independently, on *Xolotrema* by evolving enlarged, depressed shells with reduced outer lip teeth. These convergences are not very close, hence the shells are easily assigned to the correct genus.

Within a genus, the distributional pattern of shell characters among species groups and among species is generally mosaic, with many cases of convergence or parallelism. Within *Neohelix,* a parietal tooth crops up in both the *albolabris* group (some *albolabris* populations—see Pilsbry, 1940) and the *dentifera* group (*dentifera*, Fig. 29a); a basocolumellar lip node appears in both the *albolabris* group (*major,* Fig. 30c) and the *alleni* group (*alleni,* Fig. 30a); and a glossy yellowish periostracum arises in all three species groups *(albolabris hubrichti, alleni alleni,* and *lioderma).* Within *Xolotrema*, a carinate shell occurs convergently in both the *fosteri* group (*occidentalis*, Fig. 34d) and the *denotata* group (*obstricta*, Fig. 33f). Within *Triodopsis*, enlarged, flat shells with weak dentition appear in both *platysayoides* (Fig. 38) and the *tennesseensis* group (Fig. 37c–f); a squared-off parietal tooth occurs independently in the three species-groups *vulgata* (Figs. 35a, c, e, 36a), *rugosa* (Fig. 45c-), and *juxtidens* (Figs. 41c, 45a, e); a buttressed palatal tooth of identical appearance shows up in both *rugosa* of the *rugosa* group (not illustrated) and *anteridon* of the *tridentata* group (Fig. 40c); and toothless apertural lips occur convergently in three species in three disparate lineages: *platysayoides* (Fig. 38a), *soelneri* (Fig. 44c), and in rare populations of *tridentata* (see Pilsbry, 1940); a glossy periostracum appears in the *tennesseensis* group (*complanata,* Fig. 37f) and twice, ap-

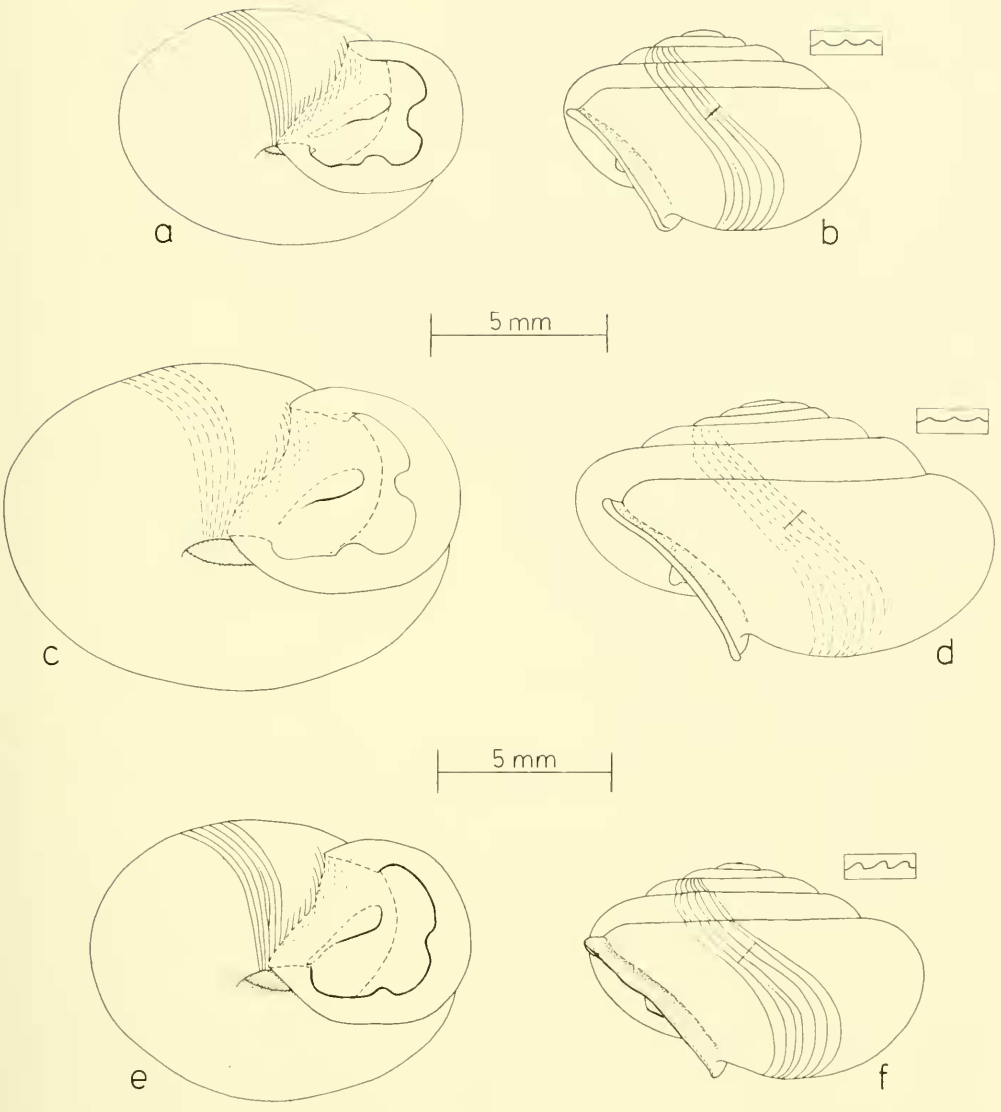

FIG. 42. Shells. **a–b.** *Triodopsis hopetonensis* (Shuttleworth, 1852). FMNH 214827 #22. **c–d.** *Triodopsis palustris* Hubricht, 1958. FMNH 214857 #1. **e–f.** *Triodopsis obsoleta* (Pilsbry, 1894). Hubricht 10300 #A.

parently independently, in the *fallax* subgroup (*palustris,* Fig. 42d; and *soelneri,* Fig. 44d). Other examples of intrageneric shell convergences among species groups and species could be cited, but these are the most conspicuous.

Shell variation within species is summarized in Table 11, which compiles Vagvolgyi's (1968) data with taxonomic corrections. Shell size, spire height, umbilical relative width, and whorl count vary greatly. Diameter range covaried significantly with sample size, whether expressed as number of lots ($r = 0.67$, d.f. = 23) or as total number of shells ($r = 0.64$, d.f. = 23). For wide-ranging, well-sampled species from all four genera (e.g., *W. multilineata, N. albolabris, X. fosteri,* and *T. tridentata*), diameter ranged approximately 70%. Maximum diameter range was found in *juxtidens:* 95%.

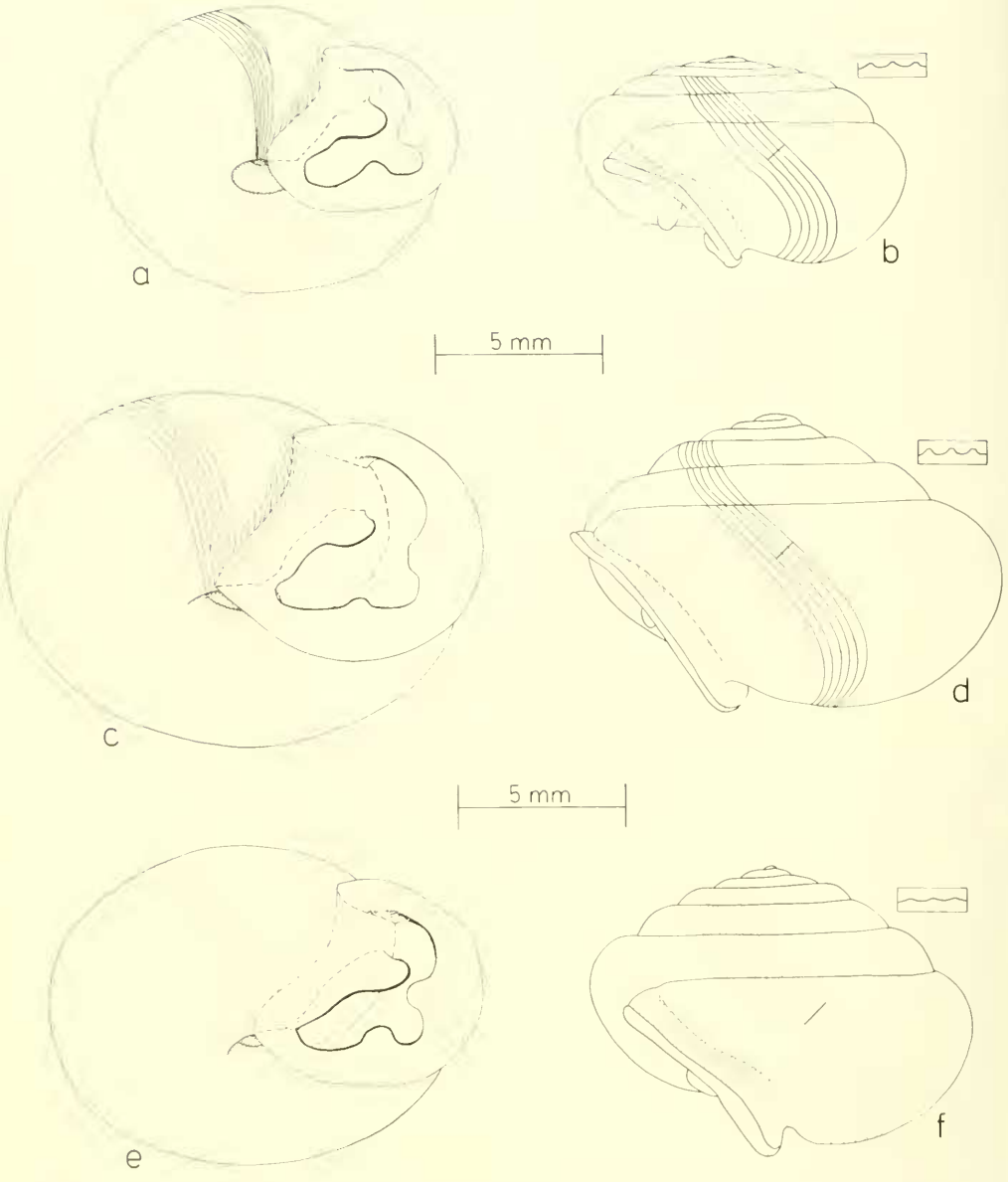

FIG. 43. Shells. **a–b.** *Triodopsis alabamensis* (Pilsbry, 1902). FMNH 214791 #A. **c–d.** *Triodopsis messana* Hubricht, 1952. FMNH 214846 #A. **e–f.** *Triodopsis vannostrandi* (Bland, 1875). FMNH 214880 #11.

DISCUSSION

Genitalic analysis

The penis proved to be an outstanding tool for the erection of a cladistic hypothesis for the eastern triodopsines. Its morphological diversity yielded an unprecedented number (for pulmonates) of character states, and its sculptural complexity permitted the detection of many convergences.

The suggested character-state transformations (Figs. 19–23) varied considerably in plausibility. The thoroughness of their documentation, however, establishes an objective baseline for future, more enlightened revisions.

The choice of PAUP (Swofford, 1983) for

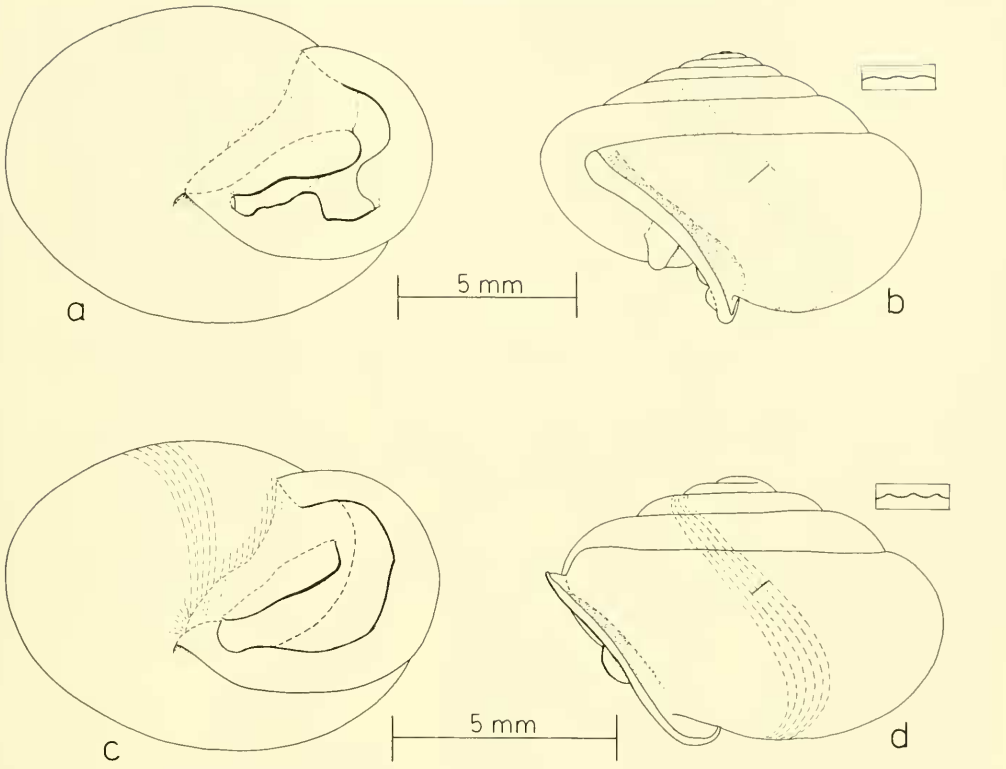

FIG. 44. Shells. **a–b.** *Triodopsis fallax* (Say, 1825). Hubricht 10209 #A. **c–d.** *Triodopsis soelneri* (Henderson, 1907). FMNH 159040 #A.

constructing cladograms has recently received support by Fink's (1986) comparisons of available software: PAUP was clearly more reliable than PHYLIP for finding the shortest trees. The Anatomy Tree generated from the triodopsine data by PAUP (Fig. 24) is remarkable for its high consistency index and for its uniqueness as the single most parsimonious cladogram. See Fink (1986) for an introduction to alternatives to the maximum-parsimony approach to cladogram construction used here.

Allozymic analysis

The number of snails electrophoresed per population averaged 3.9 (standard deviation 2.5). Although larger sample sizes would certainly have been preferred, small samples are generally sufficient for detecting systematic affinity from allozymes (Sarich, 1977; Gorman & Renzi, 1979; Shaffer, 1984; also compare the "exemplar method" of Sokal & Sneath, 1963).

Buth (1984) evaluated the available methods for applying electrophoretic data to systematics studies. Of his concluding list of 8 recommendations—(1) sample intraspecific geographic variation, (2) list raw data, (3) code allozyme data with the locus as the character for cladistic analysis, but also consider distance methods, (4) state the procedure used for ordering the transformations used for cladistic analysis, (5) construct minimum-length Wagner trees for cladistic analysis, because of their freedom from the assumption of constant evolutionary rates, (6) use outgroup comparison to determine the polarities of transformations, (7) check homoplasious steps in the constructed cladogram for possible introgressive origins, and (8) separately and identically analyze two independent data sets and examine them for congruency—all but numbers 3 and 7 were followed in this paper. Instead of Buth's number 3 recommendation to code loci as the cladistic characters, individual alleles were coded, thereby using the "independent allele model" introduced by Mickevich & Johnson (1976), "[treating] each allele as a

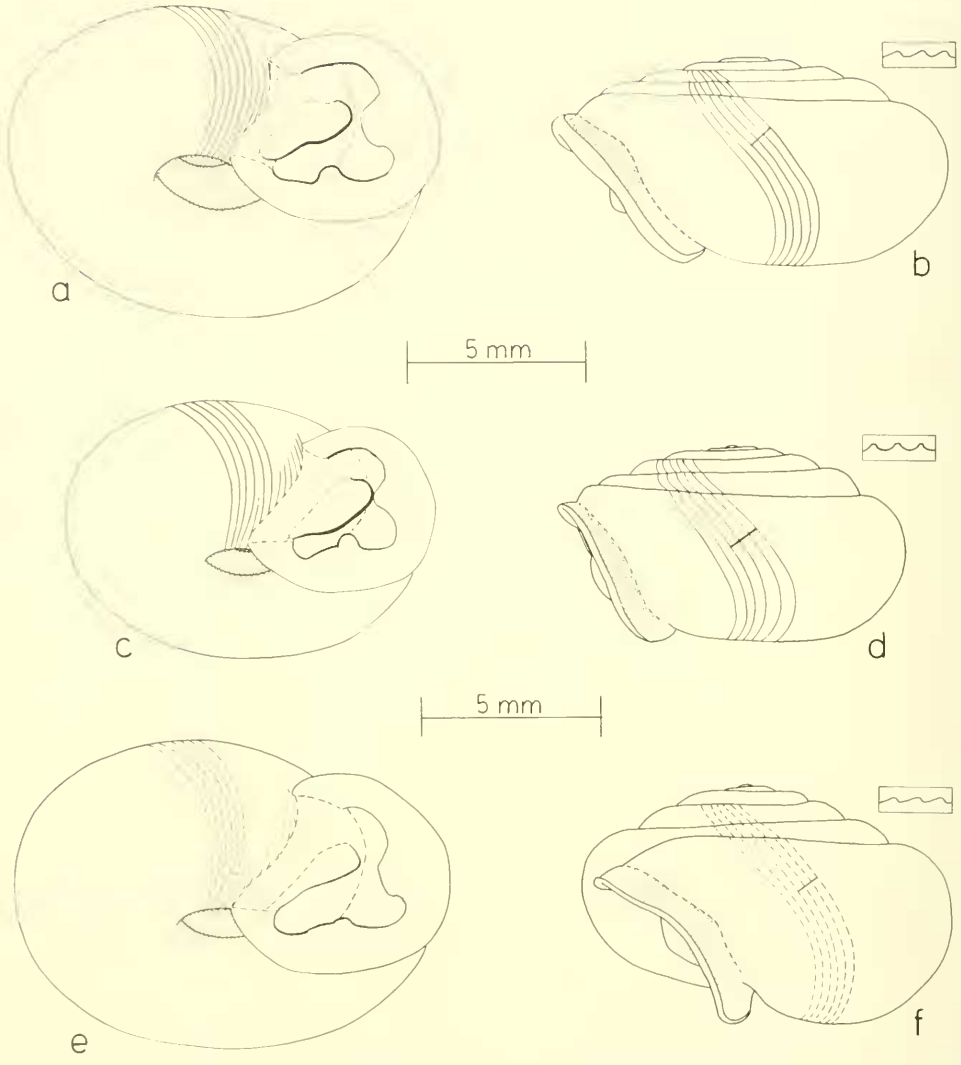

FIG. 45. Shells. **a–b.** *Triodopsis neglecta* (Pilsbry, 1899). FMNH 214850 #A. **c–d.** *Triodopsis fulciden* Hubricht, 1952. FMNH 214823 #A. **e–f.** *Triodopsis pendula* Hubricht, 1952. FMNH 214859 #14.

binary character to be scored merely as present or absent" (Mickevich & Mitter, 1981). This scoring method has the disadvantages—probably minor—of occasionally being biologically unrealistic by hypothesizing intermediates which lack alleles at a locus and by making the assumption that alleles are indeed always independent (Mickevich & Mitter, 1981). These disadvantages of the independent allele model are outweighed by its advantage of producing unquestionably ordered transformations (present/absent)—in this it differs importantly from coding the locus as the character, for which method "the problem of ordering is currently the most critical [unsolved] issue in this research area" (Buth, 1984). Of the several systems for coding independent alleles the present/absent system used in this paper is the method of choice "[when] the cladistic informativeness of frequency changes is suspect or demonstrably small" (Mickevich & Mitter, 1981), both of which conditions apply to the eastern-triodopsine data set (Table 2). Buth's number 7 recommendation to check for introgressive origins of homoplasies was not feasible for the triodopsine data set because the degree of interspecific hybridization

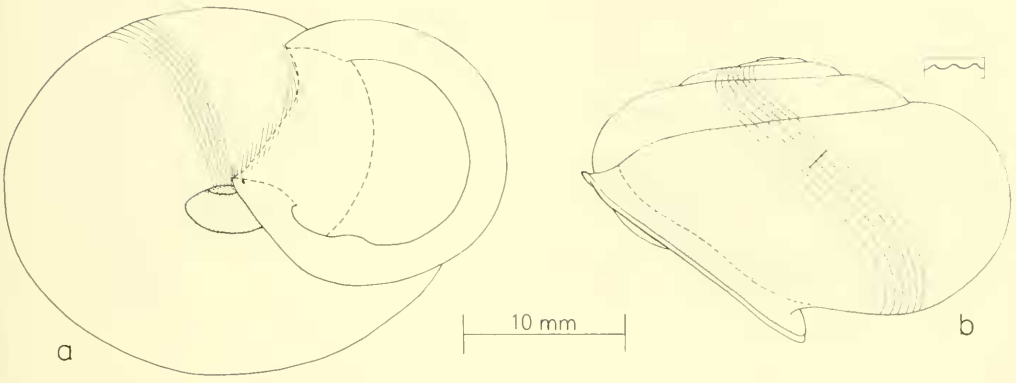

FIG. 46. *Allogona profunda* (Say, 1821). FMNH Uncat. #3. **a–b.** Shell.

TABLE 4. Measurements of penial morphology for the 6 species and subspecies of the *Neohelix albolabris* and *alleni* groups, expressed as ranges over three measured dissections (one per population). Underlined ranges are those disjunctly different from *albolabris*.

Species or subspecies	Penis length (mm)[1]	No. pilastral lappets per 2.6 mm	No. columns of pustules per 1.3 mm[2]	Verge length: penis length	Pilaster breadth: penis length	Retractor M. distance from penis apex: penis length	Vas deferens length:[3] penis length
alleni plus *fuscolabris*	10–18	15–18	9–11	.08–.09	.09–.12	.1–.3	2.1–2.4
albolabris	10–16	8–11	8–12	.15–.21	.06–.12	.4–.7	5.1–5.6
bogani	10–13	9–14	10–1	.14–.16	.07–.11	.4–.7	4.6–5.7
major	17	4–5	5–8	.12–.15	.08–.11	.4–.5	4.2–4.5
solemi	12–17	14–15	4–6	.01–.05	.02–.04	.1–.3	1.8–2.5

[1]From junction with atrium to *internal* apex.
[2]Adjacent to pilaster about two-thirds the distance from penial internal apex.
[3]From 'Y' of the atrium to insertion at penial apex.

within this group of snails is very poorly known.

The second part of Buth's (1984) number-3 recommendation to "[consider] the interpretation of distance treatments Felsenstein (1984) advanced" was followed by transforming the electrophoretic data into genetic distances, then applying a clustering algorithm. The advantages of the Prevosti genetic distance coefficient used in this analysis are its simplicity and its 0-to-1 range; the "[single] theoretical objection . . . [that it] gives equal weight to frequency differences throughout the range from 0 to 1" (Wright, 1978) does not seem critical for this data set, in which allelic frequencies can vary greatly within a species, in which heterozygosity is extremely low, and in which species usually differ by fixed, alternative alleles rather than by frequency differences among the same alleles (Table 2). The Prevosti coefficient was chosen over two which predominate in the literature—those of Nei (1972, 1978) and Rogers (1972). The failure of Nei's distance coefficient to satisfy the triangle inequality (Farris, 1981), although probably not critical theoretically (Felsenstein, 1984), can produce the practical disadvantage of negative branch lengths, "an undesirable and biologically uninterpretable result for a coefficient used in reconstructing phylogenies" (Buth, 1984). Roger's distance coefficient satisfies the triangle inequality (Buth, 1984), but has the disadvantage of being "a mixed concept depending on the degree of [allelic] fixation as well as degree of difference in such a way that two populations with fixa-

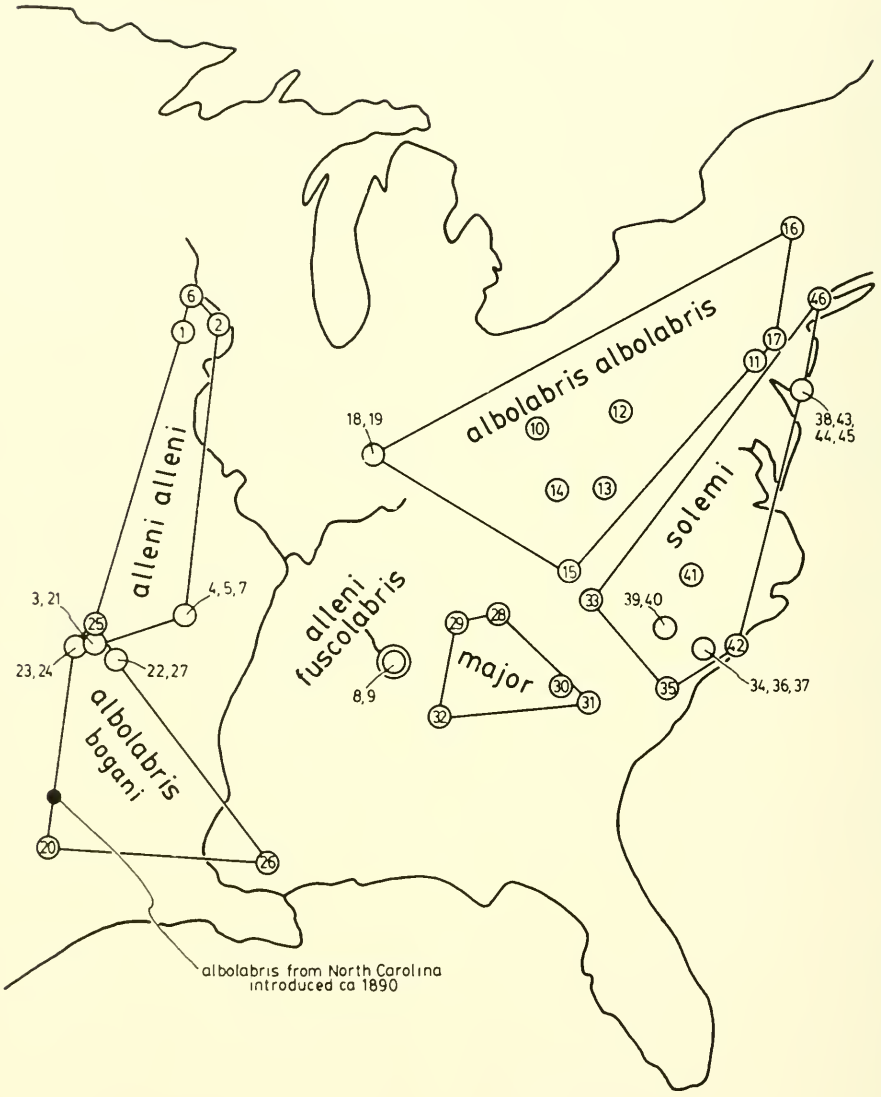

FIG. 47. Geographical distribution of the 46 populations studied for the revision of the *Neohelix albolabris* group.

tion of different alleles are considered farther apart than ones where both are heterallelic even though they have no common allele" (Wright, 1978). In retrospect, a better choice than the Prevosti coefficient would have been the Cavalli-Sforza & Edwards (1967) chord measure advocated by Wright (1978) and Felsenstein (1984).

For clustering taxa from genetic distance data, three algorithms are most commonly used: UPGMA (unweighted pair-group with arithmetic averaging: Sokal & Sneath, 1963;

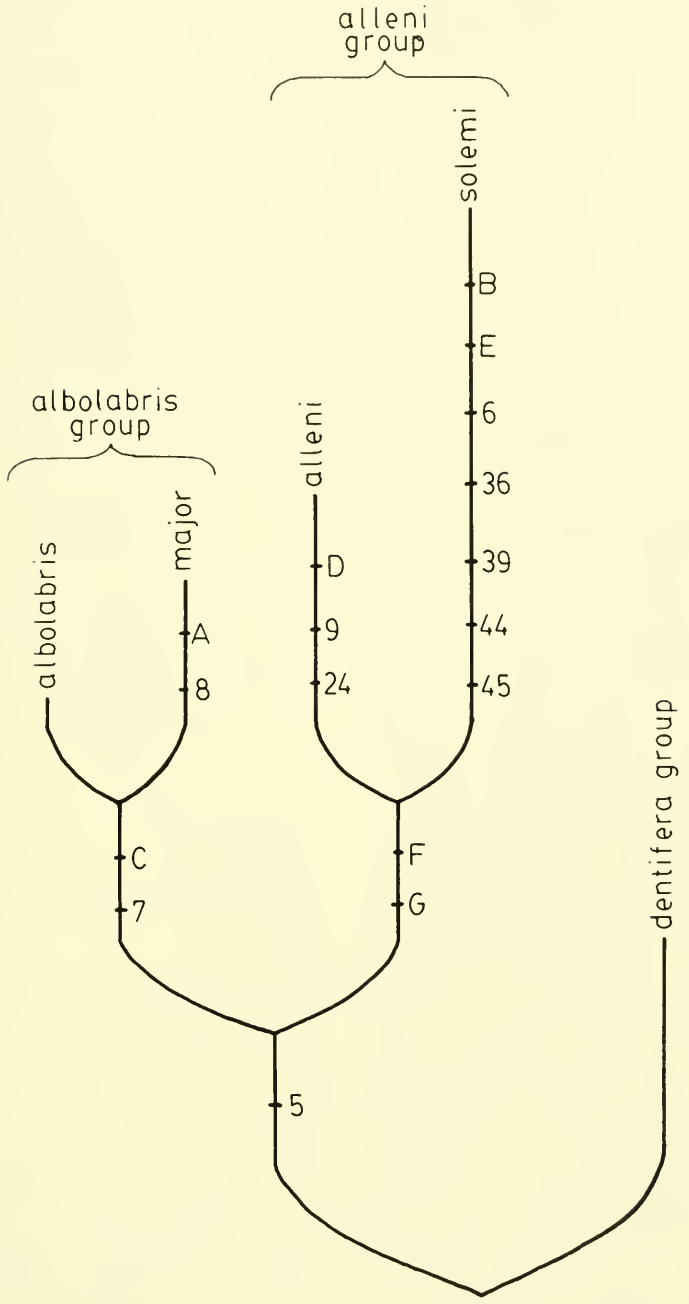

FIG. 48. Revised phylogenetic hypothesis for the *Neohelix albolabris* group, based on the addition of penial-morphological transformations A–G, with the *dentifera* group as closest outgroup. This cladogram justifies splitting the *albolabris* group into the *albolabris* and *alleni* groups.

Sneath & Sokal, 1973; Nei, 1978), Fitch-Margoliash (Fitch & Margoliash, 1967), and distance-Wagner (Farris, 1972). For this paper, the distance-Wagner procedure was chosen because it provides the best fit to the original distance data, it is free from the

TABLE 5. Shell variables used in discriminant analysis (Table 7) among the 6 species and subspecies of the *Neohelix albolabris* and *alleni* groups.

Variable	Abbreviation	Method of measurement or calculation (from Table 6)
Striae per 2.6 mm	STRIAE	Striae count (number of striae per 2.6 mm on upper surface of the end of the fifth whorl).
Brownness	BROWN	Color rank (1 to 7, ranging from light yellow to dark brown).
Glossiness	GLOSSY	Sheen rank (1 to 6, ranging from glossy to dull).
Relative height of spire	RELSPIRE	Shell height divided by shell diameter.
Whorl expansion rate	WHRLEXPN	Shell diameter divided by whorl number.
Relative size of baso-columellar node	RELNODE	Width of apertural lip at midnode, divided by width of apertural lip at its narrowest basal point.
Relative width of apertural lip	RELLIP	Width of apertural lip at periphery, divided by shell diameter.
Relative pre-apertural deflection of body whorl	RELDEFL	Body-whorl depth behind lip, minus pre-deflection body-whorl depth, divided by shell diameter.

assumption of constant evolutionary rates (unlike UPGMA and other agglomerative methods, and unlike the "Fitch-Margoliash" method of Prager & Wilson, 1978), and it is computationally feasible (unlike the true Fitch-Margoliash method) (Farris, 1981; Swofford, 1981; Tateno et al., 1982; review in Buth, 1984). Although Farris (1981) later repudiated his own distance-Wagner method (Farris, 1972) and all other methods of inferring phylogenies from distances, as inherently unable to reconstruct branch lengths consistent with evolutionary events, Felsenstein (1984) showed that "[Farris's] major criticisms of these methods lose their force" when an alternative, statistical (rather than absolute) interpretation of branch lengths is used. A drawback of the distance-Wagner algorithm is that the final tree topology is to some extent dependent on the order in which the distance data are read in for computation (e.g., Swofford & Selander, 1981). This drawback could have been (but was not for this paper) corrected by using rearrangement algorithms which shuffle and refeed the data, but even without such safeguards, "the distance-Wagner procedure is likely to be much more effective than [the Fitch-Margoliash procedure]" (Swofford, 1981).

Robustness of the consensus phylogeny

Anatomical and electrophoretic data sets were remarkably congruent. The final Consensus Tree (Figs. 28, 50) is virtually identical to the Anatomy Tree (Fig. 24), requiring little modification to comply with the electrophoretic trees (Figs. 25–27).

Thus the electrophoretic data validated the cladistic analysis of penial morphology. There is slight circularity in this statement, because *Triodopsis fraudulenta* and *T. neglecta* were anatomically reevaluated due to discrepancies between electrophoretic and anatomical data. This circularity is trivial in the context of the entire phylogeny, but it vouches strongly for the importance of comparing independent data sets to guard against misinterpretations.

Genitalic evolution: pattern and process

The results of 25 comparisons between sister taxa, presented in Table 9, showed a counter-intuitive trend. Sister taxa with virtually identical penial morphologies generally have peripatric ranges, those slightly different are generally allopatric, those moderately different are sympatric, but those greatly different are parapatric.

Several shortcomings of the data need to be considered before interpreting this result. First, two of the taxon pairs are questionable (and are so marked in Table 9), because of inadequate data or a discrepancy between anatomical and electrophoretic data. Second, those ranges were called parapatric or peripatric which appear in Fig. 49 to be contiguous or only slightly overlapping, without an intervening geographical barrier; because these maps are imprecise, some of interpretations may be incorrect. Third, current range relationships may have little relevance to those under which the anatomical changes actually evolved, because of distortion by Plio-Pleistocene and perhaps earlier climatic and vegetational changes.

If one assumes correct phylogeny and correct interpretation of temporally stable ranges, then four hypotheses concerning evolutionary processes can be proposed. (1) Peripheral isolates generally do not differentiate. (2) Vicariant isolates generally differentiate slowly. (3) Differentiation due to reproductive character displacement is moderate at most. (4) Extreme differentiation is rare, rapid, and occurs in isolates. Each of these will be discussed in turn.

Peripheral isolates generally do not appear to differentiate, because all 8 examples of peripatric sister taxa have identical genitalia (Table 9). This is consistent with the overall lack of intraspecific geographic variation found in the eastern triodopsines, as mentioned previously. There may be some natural-selected inertia to change in genital morphology due to founder effects or population bottlenecks, because these events are probably common in triodopsine species. For example, populations of *Neohelix albolabris* are patchily distributed and ephemeral, with draught and predation periodically producing local die-backs or extinctions, followed during favorable years by rapid build-ups from survivors or founders (McCracken, 1976). There would be a selective advantage to groups of *N. albolabris* in which flush-crash populations conserved ancestral genitalic morphology and were thus able to restore their genetic diversity by remating with other populations during flushes. Indeed the penial morphology of this species is remarkably uniform over its very wide geographic range (Fig. 47, Table 4).

Vicariants generally appear to differentiate slowly, because all four examples of allopatric sister taxa differ only slightly in their genitalia (Table 9). This hypothesis is further supported by two species of *Neohelix (albolabris* and *alleni),* both of which have two subspecies that have been genetically isolated by the Mississippi River (Figs. 47, 49) for at least 20,000 years (see Delcourt & Delcourt, 1981)—equivalent to at least 10,000 generations (McCracken, 1976)—and that have evolved significant shell differences (Table 7), yet are virtually identical in penial sculpture (Fig. 3, Table 4).

Differentiation due to character displacement appears to be moderate at most, because all 5 examples of sympatric sister taxa had only moderate genitalic differences, and because none of the 6 examples of sister taxa showing greater than moderate differences were sympatric. All 5 sympatric pairs are probably microsympatric. In three of them (*T. soelneri* vs. both *T. messana* and *T. hopetonensis; T. tridentata* vs. *T. juxtidens;* and *N. albolabris* vs. both *N. dentifera* and *N. divesta*) the taxa have been found within crawling distance of each other with no evidence of hybridization (personal observation); it is likely that the other two examples *(N. albolabris bogani* vs. *N. alleni alleni,* and *W. multilineata* vs. *N. albolabris)* also come into contact, with no hybrids known. In all of these cases, the penial differences were primarily in the dorsal pilaster, with occasional differences in the wall pustulation as well. These differences may be sufficient in themselves for mate recognition, but there other possible isolation mechanisms that prevent sister-species hybridization and hence that diminish the role of reproductive character displacement in causing morphological divergence. Despite Webb's (1948, 1952, 1959, 1961) conclusion that penial sculpture is the basis of mate-recognition in triodopsines, interspecific matings do occur under laboratory conditions (Grimm, 1975), even between such genitalically different species *T. tridentata* and *T. vulgata* (Webb, 1948). Thus pheromones, courtship behavior, and post-mating isolating mechanisms may also play some role in mate recognition. In addition, in some of these cases of sympatric sister species, there are varying degrees of habitat difference, suggesting that ecological character displacement limits reproductive contact. Both *W. multilineata* and *T. soelneri* inhabit marshier habitats than their sister taxa (e.g., Vagvolgyi, 1968; Hubricht 1985); *N. alleni fuscolabris* inhabits a more alkaline, limestone habitat than *N. major* (Hubricht, personal communication; personal observations); and *T. discoidea* is found on river bluffs, whereas *T. tridentata* is found in woods above the bluffs (Vagvolgyi, 1968; personal observations). No conspicuous habitat differences which would restrict contact are known for the four pairs N. alleni alleni vs. *N. albolabris hubrichti, N. divesta* vs. *N. albolabris hubrichti, N. dentifera* vs. *N. albolabris albolabris,* or *T. tridentata* vs. *T. juxtidens.* The first two of these pairs need investigation (see Solem, 1976); the third is currently under study in Virginia by T. Asami; and the fourth shows a mozaic distributional pattern (Pilsbry, 1940) suggestive of competition, although they are occasionally found microsympatric (Vagvolgyi, 1968; personal observation).

TABLE 6. Shell measurements of the *Neohelix albolabris* and *alleni* groups, from which were calculated the 8 shell variables (Table 5) used for discriminant analysis (Table 7).

Species or subspecies	Pop. no.	Shell no.	Diameter (mm)	Height (mm)	Whorl no.	Striae count*	Basal lip width**			Body whorl depth**		Color rank	Sheen rank	Notes
							At columella	At mid-node	At periphery	Pre-deflection	Behind lip			
alleni alleni	1	1	25.6	15.5	5.2	21	10	12	12	18	27	3	5	subadult
alleni alleni	2	1	27.1	16.6	5.2	18	13	13	14	23	30	3	5	subadult
alleni alleni	3	1	29.3	18.8	5.4	17	25	19	21	23	40	2	5	
alleni alleni	3	2	29.3	19.5	5.4	16	24	17	18	30	41	3	4	
alleni alleni	3	8***	30.0	18.5	5.4	19	21	16	17	23	37	2	5	subadult
alleni alleni	5	A	29.7	18.2	5.4	21	23	14	18	24	32	2	5	
alleni alleni	5	B	31.2	19.5	5.4	16	26	18	20	26	43	3	5	
alleni alleni	6	—	24.0	15.5	5.2	22	19	13	13	20	27	1	5	
alleni alleni	7	—	30.2	18.6	5.4	16	21	18	19	25	37	2	4	
alleni fuscolabris	8	7	32.9	21.1	5.6	17	32	19	20	23	30	3	4	
alleni fuscolabris	8	11	33.4	19.6	5.5	20	27	20	21	25	36	3	4	
alleni fuscolabris	9	1	34.5	20.6	5.5	20	29	18	18	15	32	3	5	
albolabris albolabris	10	A	26.5	17.3	5.7	20	22	21	21	22	32	3	3	
albolabris albolabris	10	B	27.6	18.0	5.8	20	13	13	15	20	33	2	4	subadult
albolabris albolabris	10	C	25.9	16.2	5.4	19	15	16	19	14	22	4	4	
albolabris albolabris	11	3	26.9	17.1	5.8	20	22	20	20	20	33	4	3	
albolabris albolabris	11	4***	28.0	17.5	5.8	21	17	15	16	20	34	4	4	
albolabris albolabris	12	12	29.2	18.3	5.7	23	20	22	22	20	35	5	3	
albolabris albolabris	12	14	28.2	19.3	5.6	18	23	22	22	27	43	4	3	
albolabris albolabris	12	17***	29.7	19.8	5.8	19	23	21	21	24	40	6	3	
albolabris albolabris	13	A	27.0	17.3	5.8	21	22	22	23	20	35	4	4	
albolabris albolabris	13	B	28.8	18.6	5.7	22	25	23	23	24	39	4	3	
albolabris albolabris	14	A	31.3	19.9	5.8	20	27	23	30	21	34	4	3	
albolabris albolabris	14	B	32.1	19.7	5.7	20	24	24	24	20	33	4	3	
albolabris albolabris	14	C	31.6	20.2	5.8	24	24	23	25	24	38	4	4	
albolabris albolabris	15	B	32.2	20.5	5.8	17	23	23	24	27	44	4	3	
albolabris albolabris	15	C	33.5	20.9	5.8	21	25	25	25	26	40	4	3	

albolabris hubrichti	20	1	26.4	17.0	5.6	26	16	14	15	20	34	4	5	
albolabris hubrichti	20	5	23.3	14.3	5.4	22	17	15	16	16	31	4	5	
albolabris hubrichti	20	8	26.6	17.7	5.6	25	18	15	17	21	34	4	4	
albolabris hubrichti	22	A	26.7	15.4	5.2	19	16	13	14	12	29	3	6	
albolabris hubrichti	22	B	26.8	16.9	5.5	21	15	13	16	17	31	3	6	
albolabris hubrichti	23	A	24.2	15.1	5.5	18	12	10	12	14	27	3	6	
albolabris hubrichti	23	B	23.3	15.7	5.4	22	15	13	13	18	30	3	5	
albolabris hubrichti	24	—	23.2	14.0	5.4	21	17	15	13	14	21	2	5	
albolabris hubrichti	25	—	24.3	15.4	5.4	19	10	10	10	16	24	3	6	
major	28	1	33.6	23.0	6.1	21	16	17	19	27	45	4	3	subadult
major	28	23	35.9	24.5	6.0	22	18	23	25	23	42	4	3	subadult
major	28	35	34.4	25.0	6.0	22	34	23	23	26	36	5	2	
major	29	1	32.7	21.9	6.0	23	29	19	21	26	41	4	2	
major	29	2	31.8	21.1	5.9	20	27	19	20	26	40	4	2	
major	29	3	32.6	21.6	5.8	19	30	21	23	24	42	4	1	
major	30	4	31.1	21.0	5.8	22	25	18	19	24	41	4	2	
major	30	6	29.1	18.6	5.3	22	24	19	19	18	33	4	2	
major	30	11	32.2	22.8	5.8	20	27	21	22	28	43	5	2	
major	31	A	29.2	19.5	5.5	21	27	18	17	19	35	5	2	
major	31	B	30.8	21.2	5.7	23	22	16	18	25	34	6	2	subadult
major	31	C	27.9	18.7	5.5	21	20	16	16	22	35	5	2	
solemi	32	—	34.1	23.5	5.7	22	28	23	23	32	51	4	2	
solemi	33	—	24.2	16.2	5.2	21	15	14	14	16	22	6	4	
solemi	34	—	26.0	17.5	5.5	21	13	13	14	23	35	7	4	subadult
solemi	35	—	34.6	24.3	6.1	17	22	18	18	23	44	4	3	
solemi	36	A	25.0	15.5	5.1	16	18	15	14	11	25	5	4	
solemi	36	B	23.7	16.3	5.6	21	20	20	17	20	32	4	3	
solemi	36	C	26.8	18.6	5.6	21	18	16	16	21	30	4	4	

**Number of striae per 2.6 mm on the upper surface of the end of the fifth whorl.*
***Conversion factor = .0325 mm per unit.*
****Shell misclassified by the discriminant function.*

TABLE 7. Linearized discriminant function for the *Neohelix albolabris* and *alleni* groups, based on 8 shell variables (Table 5) standardized to mean = 0 and standard deviation = 1.

	Neohelix species and subspecies					
	alleni		*albolabris*			
Shell variable	*alleni*	*fuscolabris*	*albolabris*	*hubrichti*	*major*	*solemi*
STRIAE	−1.2	−.4	−.2	.8	.7	−.7
BROWN	−3.5	−1.5	1.1	−.9	.8	1.9
GLOSSY	5.1	1.9	−.5	8.0	−10.1	−.1
RELSPIRE	.5	−1.7	−.8	.6	−.0	1.5
WHRLEXPN	1.5	4.2	−.4	−1.9	.8	−1.5
RELNODE	3.1	5.7	−2.8	−1.8	3.0	−1.9
RELLIP	1.1	−.0	2.3	−.6	−2.5	−1.5
RELDEFL	−.6	−1.9	−.3	1.2	.2	.1
Constant	−9.1	−14.4	−4.1	−9.0	−10.4	−5.2

A prediction of this hypothesis is that reproductive character displacement at the level of populations within a species should be no more than moderate, and more likely should be slight to negligible. A test of this prediction is afforded by the results of Table 10. For 12 species, penial morphology was compared between populations sympatric vs. allopatric with a species of similar shell size and shape. In not one of these comparisons was there any detectable difference. Thus the prediction is strongly confirmed, and the hypothesis is supported that differentiation due to reproductive character displacement is moderate at most.

Major differentiation appears to occur uncommonly and rapidly in isolates, because the 6 pairs of greatly different sister taxa are all parapatric, and because the other 14 pairs of isolated (non-sympatric) sister taxa are either identical or only slightly different. Thus the evolutionary pattern suggests a punctuated process: when differentiation does occur in isolates, it is extreme and rapid, leaving no intermediates.

If this hypothesis concerning major differentiation in the genitalia of eastern triodopsines is correct, then what evolutionary mechanisms produce this punctuated process? Since it occurs in parapatry, genetic drift in rare peripheral populations may have sidetracked the selectively canalized developmental program which ordinarily blocks change. Once canalization was overcome, evolutionary change could proceed by any of a number of possible mechanisms, including selection for functional optimization, sexual selection, reproductive character displacement, direct environmental selection, continued genetic drift, genetic linkage, and pleiotropism. Of these, selection for functional optimization and sexual selection seem the most likely causes of major genitalic differentiation.

Selection for functional optimization could have acted to prevent the loss of sperm during transfer due either to (1) the penis slipping out or (2) the sperm being captured and digested by the mate's gametolytic gland (the spermatheca—see Tompa, 1984). These two selective pressures would have favored both sculptural modifications which improved the penis's frictional hold within the mate's gametolytic duct (the functional vagina), and structural modifications which improved the ejected sperm's chances of escaping back down this duct to reach the fertilization pouch (the talon—see Tompa, 1984). It seems reasonable that these selective pressures were responsible for such conspicuous features as (1) the grappling-hook-like pilaster of the *Triodopsis tennesseensis* group (Fig. 11b–d); (2) the chevron-like patterns of wall pustules convergent among the *Xolotrema fosteri-denotata* (Figs. 7, 8), the *Triodopsis platysayoides* (Fig. 12), and the *Triodopsis cragini-tridentata-juxtidens* (Figs. 13–18) lineages; (3) the backward-directed verge in *Webbhelix* (Fig. 6a) and *Neohelix* (Figs. 2–5); and (4) the clubbed apex with a subterminal ejaculatory pore convergent among the *Neohelix solemi* (Fig 6b), the *Xolotrema denotata* (Fig. 7), the *Triodopsis vulgata* (Fig. 9), and the *Triodopsis tridentata-fallax-juxtidens* (Figs. 14–18) lineages (see Fig. 50). Convergences in these structures probably indicate that they are adaptive.

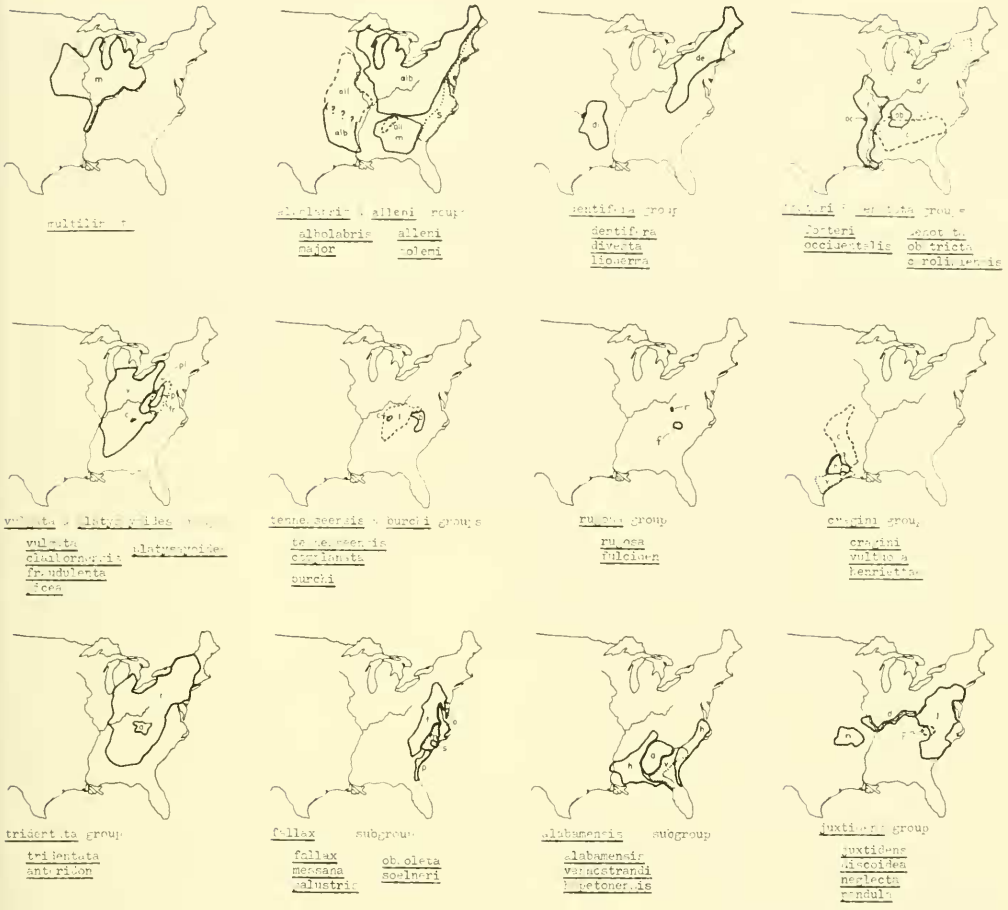

FIG. 49. Range maps of eastern American triodopsines. Adapted from Hubricht (1985).

If these suggestions are correct, why, then, is there so much diversity of form? That is, why are so many different responses to the same two selective pressures? In the first place, the selective pressures may not be equal in each clade. For example, one clade may have a thick mucus which would clog delicate sculpture and therefore would select for coarse sculpture. Or, for example, clades may differ in the strength of the digestive enzymes secreted by the gametolytic gland or in the presence or strength of a muscular pump in the wall of the gametolytic duct (the functional vagina), therefore selecting differently for morphological "strategies" to channel the ejaculate back down the duct.

According to the hypothesis of sexual selection by female choice, "male genitalia function as 'internal courtship' devices used by females to discriminate among "males" (Eberhard, 1986). Runaway sexual selection produces rapid and *arbitrary* divergence in penial morphology, according to Eberhard's model. Much of the divergence in eastern-triodopsine genitalia, however, is not arbitrary but is convergent, suggesting natural selection for function rather than sexual selection. Both forms of selection have probably played a role, however. Certainly the apparent rapidity of divergence is consistent with Eberhard's model.

Reproductive character displacement has already been ruled out as a likely cause of major differentiation.

TABLE 8. Comparison of the revised classification of eastern American triodopsines with three previous classifications.

This classification				Pilsbry's (1940) classification			Webb's (1952, 1954a, 1959) classification			Vagvolgyi's (1968) classification		
Genus	Species group	Species subgroup	Species	Subgenus	Species	Subspecies	Genus	Subgenus	Section	Subgenus	Species	Subspecies
Webbhelix	—	—	*multilineata*	*Neohelix*	*multilineata*	—	*Xolotrema*	*Neohelix*	—	*Neohelix*	*multilineata*	—
Neohelix	*albolabris*	—	*albolabris*	*Neohelix*	*albolabris*	*albolabris*	*Xolotrema*	*Neohelix*	—	*Neohelix*	*albolabris*	*albolabris*
Neohelix	*albolabris*	—	*major*	*Neohelix*	*albolabris*	*major*	*Xolotrema*	*Neohelix*	—	*Neohelix*	*albolabris*	*major*
Neohelix	*alleni*	—	*alleni*	*Neohelix*	*albolabris*	*alleni & fuscolabris*	*Xolotrema*	*Neohelix*	—	*Neohelix*	*albolabris*	*alleni*
Neohelix	*alleni*	—	*solemi*	*Neohelix*	*albolabris*	*traversensis*	—	—	—	—	—	—
Neohelix	*dentifera*	*dentifera*	*dentifera*	*Neohelix*	*dentifera*	—	—	—	—	*Neohelix*	*dentifera*	—
Neohelix	*dentifera*	*divesta*	*divesta*	*Neohelix*	*divesta*	—	*Xolotrema*	*Neohelix*	—	*Neohelix*	*divesta*	—
Neohelix	*dentifera*	*divesta*	*lioderma*	*M. (Mesodon)*	*indianorum*	*lioderma*	—	—	—	—	—	—
Xolotrema	*fosteri*	—	*fosteri*	*Xolotrema*	*fosteri*	—	*Xolotrema*	*Wilcoxorbis*	—	*Xolotrema*	*fosteri*	*fosteri*
Xolotrema	*fosteri*	—	*occidentalis*	*Xolotrema*	*obstricta*	*occidentalis*	—	—	—	*M. (Patera)*	*sargentianus*	*occidentalis*
Xolotrema	*denotata*	—	*denotata*	*Xolotrema*	*notata*	—	*Xolotrema*	*Xolotrema*	—	*Xolotrema*	*obstricta*	*denotata*
Xolotrema	*denotata*	—	*obstricta*	*Xolotrema*	*obstricta*	—	—	—	—	*Xolotrema*	*obstricta*	*obstricta*
Xolotrema	*denotata*	—	*caroliniensis*	*Xolotrema*	*caroliniensis*	—	—	—	—	*Xolotrema*	*obstricta*	(hybrid)
Triodopsis	*vulgata*	*vulgata*	*vulgata*	*Triodopsis*	*fraudulenta*	*vulgata*	*Triodopsis*	*Triodopsis*	*Shelfordorbis*	*Triodopsis*	*neglecta*	*vulgata*
Triodopsis	*vulgata*	*vulgata*	*claibornensis*	—	—	—	—	—	—	*Triodopsis*	*neglecta*	*vulgata*
Triodopsis	*vulgata*	*fraudulenta*	*fraudulenta*	*Triodopsis*	*fraudulenta*	—	—	—	—	*Triodopsis*	*fraudulenta*	—
Triodopsis	*vulgata*	*fraudulenta*	*picea*	—	—	—	—	—	—	*Triodopsis*	*fraudulenta*	—
Triodopsis	*platysayoides*	—	*platysayoides*	*Triodopsis*	*platysayoides*	—	—	—	—	*Triodiopsis*	*complanata*	*platysayoides*
Triodopsis	*burchi*	—	*burchi*	—	—	—	—	—	—	*Triodopsis*	*burchi*	—
Triodopsis	*tennesseensis*	—	*tennesseensis*	*Triodopsis*	*tridentata*	*tennesseensis*	—	—	—	*Triodopsis*	*complanata*	—
Triodopsis	*tennesseensis*	—	*complanata*	*Triodopsis*	*tridentata*	*complanata*	—	—	—	*Triodopsis*	*complanata*	—
Triodopsis	*rugosa*	—	*rugosa*	*Triodopsis*	*rugosa*	—	—	—	—	*Triodopsis*	*rugosa*	—
Triodopsis	*rugosa(?)*	—	*fulciden*	—	—	—	—	—	—	*Triodopsis*	*fulciden*	—
Triodopsis	*cragini*	—	*cragini*	*Triodopsis*	*cragini*	—	*Triodopsis*	*Haroldorbis*	—	*Triodopsis*	*copei*	*cragini*
Triodopsis	*cragini*	—	*vultuosa*	*Triodopsis*	*vultuosa*	—	—	—	—	*Triodopsis*	*copei*	(hybrid)
Triodopsis	*cragini*	—	*henriettae*	*Triodopsis*	*vultuosa*	*henriettae*	—	—	—	*Triodopsis*	*copei*	(hybrid)
Triodopsis	*tridentata*	—	*tridentata*	*Triodopsis*	*tridentata*	—	*Triodopsis*	*Triodopsis*	—	*Triodopsis*	*tridentata*	—
Triodopsis	*tridentata*	—	*anteridon*	*Triodopsis*	*rugosa*	*anteridon*	—	—	—	*Triodopsis*	*rugosa*	—
Triodopsis	*fallax*	*fallax*	*fallax*	*Triodopsis*	*fallax*	—	—	—	—	*Triodopsis*	*fallax*	*fallax*
Triodopsis	*fallax*	*fallax*	*messana*	—	—	—	—	—	—	*Triodopsis*	*fallax*	(hybrid)
Triodopsis	*fallax*	*fallax*	*palustris*	—	—	—	—	—	—	*Triodopsis*	*fallax*	*obsoleta*
Triodopsis	*fallax*	*fallax*	*obsoleta*	*Triodopsis*	*hopetonensis*	*obsoleta*	—	—	—	*Triodopsis*	*fallax*	*obsoleta*
Triodopsis	*fallax*	*fallax*	*soelneri*	*Triodopsis*	*soelneri*	—	—	—	—	*Triodopsis*	*soelneri*	—
Triodopsis	*fallax*	*alabamensis*	*alabamensis*	*Triodopsis*	*vannostrandi*	*alabamensis*	—	—	—	*Triodopsis*	*fallax*	*alabamensis*
Triodopsis	*fallax*	*alabamensis*	*vannostrandi*	*Triodopsis*	*vannostrandi*	—	*Triodopsis*	*Triodopsis*	—	*Triodopsis*	*fallax*	(hybrid)
Triodopsis	*fallax*	*alabamensis*	*hopetonensis*	*Triodopsis*	*hopetonensis*	—	*Triodopsis*	*Triodopsis*	—	*Triodopsis*	*fallax*	(hybrid)
Triodopsis	*juxtidens*	*juxtidens*	*juxtidens*	*Triodopsis*	*tridentata*	*juxtidens*	*Triodopsis*	*Triodopsis*	—	*Triodopsis*	*juxtidens*	*juxtidens*
Triodopsis	*juxtidens*	*juxtidens*	*discoidea*	*Triodopsis*	*tridentata*	*discoidea*	*Triodopsis*	*Triodopsis*	—	*Triodopsis*	*juxtidens*	*discoidea*
Triodopsis	*juxtidens*	*neglecta*	*neglecta*	*Triodopsis*	*neglecta*	—	*Triodopsis*	*Triodopsis*	—	*Triodopsis*	*neglecta*	*neglecta*
Triodopsis	*juxtidens*	*neglecta*	*pendula*	—	—	—	—	—	—	*Triodopsis*	*pendula*	—

TABLE 9. Comparison of the difference in penial morphology with the relationship between geographic ranges for 25 pairs of sister taxa of eastern triodopsines according to the phylogeny in Fig. 50. The taxa are designated by five-letter abbreviations. Question marks denote pairs of phylogenetically uncertain status. "−" is a minus sign.

Phylogenetically adjacent taxa	Penial shift	Geographical relationship
solem vs. rest of Neohelix	great	parapatric
fostr group vs. denot group	great	parapatric
platy vs. vulgt group	great	parapatric
tenns group vs. burch group (?)	great	parapatric
cragn group vs. rugos group	great	parapatric
cragn group vs. tridt group	great	parapatric
Webbhelix vs. Neohelix-solem	moderate	sympatric
soeln vs. rest of fallx subgroup	moderate	sympatric
tridt group vs. juxtd group	moderate	sympatric
dentf group vs. albol group + allen	moderate	sympatric
albol group vs. allen	moderate	sympatric
albol vs. major	slight	allo or parapatric
dentf group vs. divst group	slight	allopatric
vulgt subgroup vs. fraud subgroup	slight	allo or parapatric
rugos vs. fulcd (?)	slight	allopatric
liodm vs. divst	none	peripatric
occdt vs. fostr	none	peripatric
denot group (3 spp.)	none	paraipatric
claib vs. vulgt	none	peripatric
picea vs. fraud	none	peripatric
compl vs. tenns	none	peripatric
cragn group (3 spp.)	none	peripatric
fallx subgroup-soeln (7 spp.)	none	parapatric
anter vs. tridt	none	peripatric
juxtd group (4 spp.)	none	peri or allopatric

Did the external environment select for penial-morphological differences in the eastern triodopsines? It seems unlikely. The species groups and genera—that is, the major morphological types—do not segregate ecologically (Emberton, 1986), nor is there any evidence of environmental correlation at any level, including within species groups. There seems to be no correlation between the size of the penis and its structural complexity. For example, *Neohelix lioderma* is as small in both body and penis as many species of *Triodopsis,* yet has the *Neohelix* penial sculpture in its full complexity (Fig. 5a). A correlation recurrent in stylommatophorans between arid habitat and short penial length (Solem, personal communication) does not apply to the eastern triodopsines, in which the greatest penis-length-to-shell-diameter ratio occurs in the *Triodopsis cragini* group (Fig. 13), which also occupies the most arid habitat of all known triodopsines (Emberton, 1986).

Genetic drift, although possibly the instigator of genitalic divergence by straying from canalized fitness peaks, is not likely to be the proximate cause of the divergence. Evidence for this view lies in the multiple convergences and in the apparent speed and morphological precision of evolution. Drift, however, can be held responsible for vestigialization: random variation in structures that are no longer functional. The dorsal pilaster of *Neohelix solemi* (Fig. 6b), as well as the verges of *N. solemi,* the *Xolotrema fosteri* group (Fig. 8), and the *Xolotrema denotata* group (Fig. 7), are presumably vestigial.

Although the rough concordance between conchology and penial morphology (Fig. 50) could indicate genetic linkage, with selective changes in the shell randomly inducing unselected changes in the penis, it is more likely that since both shell and genitalia have undergone (independent) evolutionary divergence, they both are correlated with time, and hence, secondarily, with each other. Eastern triodopsines have a relatively high chromosome number (29 to 32 pairs, according to Husted & Burch, 1947), obviating the ne-

TABLE 10. The localities (state:county) of populations dissected in searches for reproductive character displacement between pairs of conchologically similar species of eastern American triodopsines. The number of specimens dissected from each population is in parentheses.

Species A	Allopatry	Sympatry	Allopatry	Species B
albolabris	AR:Logan(1) AR:Washington(1) OK:Sequoyah(3) TX:Houston(3) LA:Washington(1)	AR:Crawford(2,3)	AR:Izard(8) IA:Lynn(1) IA:Jackson(1) IA:Clayton(1)	*alleni*
albolabris	WV:Greenbrier(2) WV:Boone(3) NC:Watauga(3) OH:Athens(2) PA:Chester(2)	WV:Preston(3,3)	WV:Pendleton(3)	*dentifera*
vulgata	KY:Harlan(4) TN:Morgan(2)	KY:Fayette(1,3&3)	—	*denotata* & *tennesseensis*
vulgata	KY:Fayette(1) TN:Morgan(2)	KY:Harlan(1,4)	KY:Edmonson(2) WV:Pendleton(1) WV:Pocahontas(1) WV:Preston(1) OH:Athens(3)	*tridentata*
tridentata	KY:Harlan(1) WV:Pocahontas(1) WV:Pendleton(1) WV:Preston(1) OH:Athens(3)	KY:Edmonson(2,2)	—	*obstricta*
tridentata	WV:Pocahontas(1) WV:Preston(1) KY:Edmonson(2) KY:Harlan(1) OH:Athens(3)	WV:Pendleton(1,2)	—	*picea*
juxtidens	WV:Pendleton(2) NC:Catawba(3) NC:Burke(1)	WV:Pocahontas(2,1)	WV:Pendleton(1) WV:Preston(1) KY:Edmonson(2) KY:Harlan(1) OH:Athens(3)	*tridentata*

cessity for, or the probability of, tight linkages.

Pleiotropy is also an unlikely explanation for the major morphological diversity of the eastern-triodopsine penis because the penis develops from mesoderm, whereas the shell-forming mantle develops from ectoderm (Raven, 1975).

To summarize, neither reproductive character displacement, environmental selection, genetic drift, genetic linkage, nor pleiotropy is a probable cause of major evolutionary change in eastern-triodopsine genitalia. This supports the suggestion that selection for functional optimization and sexual selection are the most likely causes.

Shell evolution: pattern and process

Since the consensus phylogeny (Figs. 28, 50) was constructed strictly from soft-part anatomy and biochemistry, there is no circularity in using it to detect patterns of shell evolution. Shell variation was analyzed at three taxonomic levels: among genera, among species groups, and within species groups. Patterns—and inferred processes—of variation differ among these levels.

In general, each genus has a characteristic shell morphology (Fig. 50). *Neohelix* and *Webbhelix* share the plesiomorphous shell: large, globose, and toothless. *Xolotrema* shells are medium-sized and depressed, with

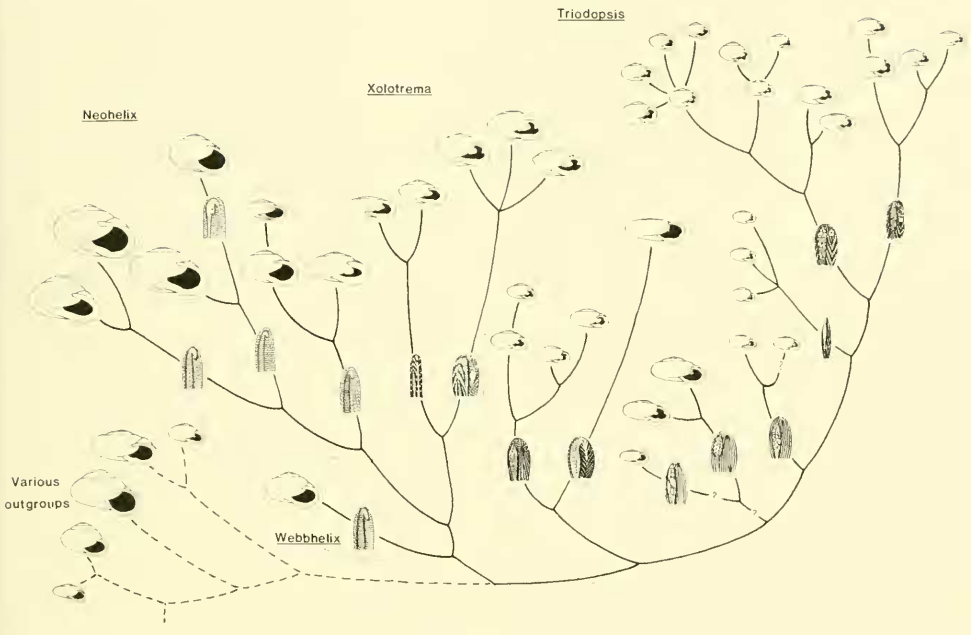

FIG. 50. Evolution of shell morphology and of upper penial sculpture in eastern American triodopsines.

a blade-like parietal tooth and a long basal lamella. *Triodopsis* shells are small, subglobose, and tridentate. The most common exceptions to this generality are in size. Intraspecific variation—discussed below—produces broad overlap in shell size, both within and between genera. Nevertheless, the largest occur in *Neohelix,* and by far the smallest occur in *Triodopsis.* The rare convergences (*Neohelix dentifera, Triodopsis platysayoides,* and the *T. tennesseensis* group) offer little contradiction to the generality that within major clades (genera) of eastern triodopsines, shell morphology is distinct and virtually static.

The evolutionary process behind this pattern is problematic. A preliminary study (Emberton, 1986) concluded that the genera broadly overlap ecologically, with virtually no conchological changes accompanying ecological convergences. Ecological relationships are clearly in need of further investigation (see Goodfriend, 1986).

Within a genus, the distributional pattern of shell characters among species groups is generally mosaic, with many cases of convergence or parallelism. This rank mosaicism has confused past conchologically based systematics (e.g. Pilsbry, 1940, and Vagvolgyi, 1968; see Table 8). Its pattern suggests a process encompassing both drift and selection. Possible selective explanations for a few of the recurrent shell features are discussed in the next section. For many of these features, however, it seems more likely—but would be impossible to demonstrate unequivocally—that their genetic program is ubiquitous in the subgenus, is selectively neutral with respect to its alternative states, and is expressed randomly among species of the clade due to genetic drift. This process is called genetic indeterminism by Throckmorton (1965)—also see Gould's (e.g. Gould & Woodruff, 1986) discussions of morphological canalization.

Within species, there is great variation in shell size, spire height, umbilical relative width, and whorl count (Table 11). Diameter ranges up to 95% within a species; the extent of this range in shell size depends on the number of populations and specimens measured. Such variation in adult size is common not only in land snails, whose time for shell growth (before it is interrupted by reproductive maturity) depends heavily on the local humidity regime (e.g., Solem & Christensen,

TABLE 11. Ranges of variation in shell measurements in species of eastern triodopsines. Compiled from the text of Vagvolgyi (1968), with taxonomic adjustments according to Table 8.

Species	Lots	Shells per lot	Total shells	Diameter	Diameter range	Height	Ht/diam	Umbilicus	Um/diam	Whorls	Whls/diam
multilineata	32	2–25	230	16.2–28.1	73.5%	10.0–18.2	.55–.71	0	0	—	—
albolabris + (solemi)	86	1–21	468	20.2–35.6	76.2%	11.5–23.9	.52–.73	0	0	—	—
major + (solemi)	19	1– 8	41	27.1–41.7	53.9%	18.8–30.5	.62–.74	0	0	—	—
alleni	10	2–17	57	23.3–30.1	29.2%	13.7–17.8	.55–.64	0	0	—	—
dentifera	13	1– 5	24	19.5–27.6	41.5%	10.6–15.6	.52–.57	0	0	—	—
divesta	7	1–13	24	16.9–19.5	15.4%	8.7–11.8	.49–.67	0	0	—	—
fosteri	23	2–12	116	13.8–22.0	59.4%	6.9–11.0	.43–.58	0	0	4.6–5.5	.25–.35
denotata	42	2–24	197	17.0–25.9	52.4%	8.5–12.9	.42–.57	0	0	4.8–5.8	.21–.30
obstricta	11	2– 7	41	19.7–25.9	31.5%	9.6–12.6	.41–.56	0	0	5.2–5.8	.22–.27
vulgata + claibornensis	37	1–25	231	12.2–19.8	62.3%	5.8–10.6	.41–.63	2.4–5.1	.16–.30	5.0–6.4	.30–.45
fraudulenta + picea	9	1–10	34	12.7–16.9	33.1%	6.7– 9.0	.45–.63	1.9–3.9	.15–.24	5.2–6.1	.34–.43
burchi	3	2–15	29	8.9–13.2	48.3%	4.9– 6.2	.45–.56	1.5–2.7	.15–.21	—	—
tennesseensis + complanata	22	1–11	65	16.7–23.3	39.5%	8.0–10.6	.40–.54	2.9–6.0	.17–.26	—	—
rugosa + anteridon	13	1– 8	44	10.6–15.5	46.2%	5.4– 7.2	.42–.54	1.7–3.6	.16–.23	—	—
cragini	16	2–12	83	7.7–10.8	40.3%	3.7– 6.7	.48–.67	1.1–2.0	.13–.19	4.3–5.5	.47–.60
vultuosa	5	2– 7	16	11.5–14.5	26.1%	6.1– 7.5	.48–.60	1.9–4.0	.17–.28	5.3–6.0	.41–.50
tridentata	80	1–15	395	12.3–20.7	68.3%	5.5–11.0	.43–.57	2.0–4.3	.14–.24	—	—
fallax	20	2–30	187	10.1–15.5	53.5%	5.9– 9.1	.50–.66	1.3–3.2	.12–.22	5.0–6.6	.38–.56
palustris + obsoleta + (fallax)	24	2–31	434	9.7–13.5	39.2%	5.1– 8.8	.47–.65	1.2–2.7	.11–.22	4.5–6.0	.39–.53
alabamensis	15	2–27	144	8.6–13.1	52.3%	4.9– 7.5	.48–.66	1.2–3.0	.12–.24	5.1–7.0	.49–.68
juxtidens	38	1–32	282	9.8–19.1	94.9%	5.3– 9.9	.46–.61	1.1–3.5	.12–.49	—	—
discoidea	13	3–15	94	12.9–20.9	62.0%	5.8–10.0	.40–.54	2.2–4.6	.14–.23	—	—
neglecta	9	1–30	81	9.9–13.2	33.3%	4.6– 6.5	.41–.53	2.1–3.9	.20–.30	4.8–6.0	.40–.51
pendula	9	1–10	34	10.7–13.8	29.0%	5.5– 7.2	.50–.59	2.0–3.2	.19–.25	4.9–5.8	.41–.49

1984; Gould, 1985), but also in aquatic gastropods (e.g., Vermeij, 1980).

Vagvolgyi (1968) documented that intraspecific shell variation is geographically patchy and non-clinal (the small number of clines he reported is no more than one would expect by chance). The same was true of apertural features, keel, fulcrum, and sculpture. Vagvolgyi attributed this patchy variation to ecophenotypic responses to patchily distributed microclimates, "occur[ing] in spite of gene flow, not because of lack of it." This interpretation is probably correct—see the documentation of this phenomenon in *Cerion* (Gould, 1985) and in *Neohelix major* and *Mesodon normalis* (Emberton, 1986))—but genetic drift and local selection could also play significant roles.

In addition to this patchy, non-clinal pattern in size and shape, there are several correlations between niche and shell morphology which recur within species and species groups. These convergences, discussed in turn below, are probably due to environmental selection.

Apertural obstruction correlates with ground moisture. Parallel altitudinal clines in the size of apertural teeth occur in *Triodopsis tridentata, T. fallax,* and *T. fraudulenta* (Vagvolgyi, 1968). The aperture becomes more obstructed with increasing elevation and, concomitantly, increasing ground moisture. An altitudinally opposite cline exists in the *cragini* group (Vagvolgyi, 1968), with the most highly obstructed species *(henriettae)* inhabiting lowland, riverine forests; the least obstructed species *(cragini)* occupying dry uplands; and *vultuosa* intermediate in both apertural obstruction and habitat. Thus the consistent correlation in all four clines is with ground moisture. This pattern supports the view of apertual teeth as barriers to insect predators, presuming that the density and/or diversity of insect predators increases with increasing ground moisture, but fails to support the view of apertural denticles as barriers to water loss (Goodfriend, 1986). An alternative view is that snails living in humid habitats have a longer season of activity, hence more time for the deposition of shell material, including the apertural teeth.

Flatness correlates with crevice dwelling. Five separate species groups show the parallel evolution of a flat-spired species associated with rock crevices (see Emberton, 1986). In the *Neohelix alleni* group, *N. alleni fusco-labris* is flat for the group, and is restricted to limestone-cliff areas of northern Alabama and adjacent Tennessee (Hubricht, 1985, and personal communication; personal observations). The *Xolotrema fosteri* group has *X. occidentalis,* a flat, subcarinate cliff-dweller; the *Xolotrema denotata* group has *X. obstricta,* which, with its pronounced keel and depressed spire, is the most rock-associated member of its group. The aberrant *Triodopsis platysayoides* inhabits crevices between sandstone blocks in a restricted region of the New River Gorge, West Virginia, and has the flattest spire of the entire genus. The *Triodopsis juxtidens* group's only exclusive cliff-dweller (along the Ohio River Valley) is the conspicuously flat *T. discoidea.* This parallel concordance with habitat suggests that a flat shell is adaptive for rock-crevice dwelling. Similar environmental correlations occur in several lineages of Mediterranean helicids, suggesting the same selective pressures (Goodfriend, 1986).

Glossiness correlates with water. Another iterated shell-habitat correlation—pointed out by Vagvolgyi (1968), and comparable, as he stated, to Rensch's (1932) trends—is between a glossy periostracum and nearness to a large body of water. The glossiest member of the *Neohelix dentifera* group *(N. lioderma)* appears to be restricted to the Arkansas River Valley. In the *Triodopsis tennesseensis* group, glossy *T. complanata* lives along the river, whereas dull *T. tennesseensis* occurs on the upper banks and farther inland. In the *Triodopsis fallax* group, two species have independently evolved a shiny periostracum: *T. palustris* along the Santee River floodplain, and *T. soelneri* in the marshes of the Lake Waccamaw area. The riverine cliff snail *Triodopsis discoidea* is the glossiest member of the *T. juxtidens* group. Glossiness may be an exclusively ecophenotypic effect, but is probably at least a partially selected trait. Its heritability has never been assessed, although Grimm's (1975) lab-reared *T. soelneri* and its hybrids should yield important data (see Appendix D).

Juvenile apertural size correlates with aridity. Vagvolgyi (1968) also noted that arid-adapted species of eastern triodopsines have relatively smaller juvenile apertures, hence the tightly coiled shells of the *Triodopsis alabamensis* group and, to a lesser extent, the *Triodopsis cragini* group. The same pattern has been found in various other groups of land snails; it implies natural selection for water loss, although not all experimental re-

sults have been consistent with this interpretation (Goodfriend, 1986).

To summarize, there are two major components to the pattern of shell variation within species and species groups of eastern triodopsines, and they appear to differ in the processes which produced them. First, the patchy, non-clinal variation in the size, and many features of form, of the shells is probably due to ecophenotypic effects. And second, the several correlations between environment and shell morphology iterated among separate lineages are probably due primarily to natural selection, with perhaps some ecophenotypic contribution.

What is a species in the eastern American triodopsines?

If the biological species concept were used for the eastern triodopsines, species groups would probably be reduced to species. Species groups have, with two exceptions *(Neohelix solemi* and *Triodopsis soelneri),* virtually identical genitalia, hence are probably capable of interbreeding. Indeed, hybridization has been reported (based on analysis of geographical shell variation) within the *Xolotrema denotata* group (Vagvolgyi, 1968) and the *Triodopsis fallax* group (Hubricht, 1953; Vagvolgyi, 1968; Grimm, 1975). Vagvolgyi (1968) even concluded that certain Hubrichtian (1985) species are not species at all, but hybrid swarms: *X. caroliniensis, T. vultuosa, T. henriettae, T. messana, T. vannostrandi,* and *T. hopetonensis.* The only reported cases of reproductive isolation within species groups occurs among some members of the *Triodopsis fallax* group, which nevertheless still hybridize in the laboratory (Grimm, 1975; see Appendix D). Laboratory hybridization has also been reported within the *Xolotrema denotata* group (Webb, 1980).

In the revision of the *Neohelix albolabris* and *alleni* groups (Appendix B), the biological species concept was applied, using the "yardstick method" of comparing sympatric species to determine the degree of penial difference capable of reproductively isolating species (under the still unproven assumption that penial morphology is the predominant mate-recognition system). Thus, subspecific status was assigned to genetically isolated, conchologically differentiated taxa which had the same or only minutely different penial sculpture. Specific status was provisionally assigned to *N. major* because its penis may be different enough, by yardstick criteria, from the similar *N. albolabris* to prevent interbreeding, and this difference is disjunct, with no sign of clinal intergradation. If these same criteria were applied to a species-level revision of all eastern triodopsines, then species groups would be reduced to species.

This was not done for a number of reasons. First, there are important precedents in land-snail taxonomy for species which hybridize. Gould & Woodruff (1986), for example, opted to assign specific status to two hybridizing "semispecies" of snails *(Cerion glans* and *gubernatorium)* of New Providence Island because of a multitude of evolutionarily significant differences. Murray & Clarke (e.g., 1980) followed a similar taxonomic path with the "incipient species" of *Partula* on Moorea.

Second, there is some evidence that species may be reproductively isolated despite close genitalic and conchological similarities. Recent discoveries in the confamilial genus *Ashmunella* indicate that morphological differences among valid species can be slight. *Ashmunella* has all appearances of being oversplit, with specific status bestowed on a mosaic collection of often subtle shell difference. Karyotypic and breeding studies (Babraksai & Miller, 1984) have shown, however, that at least one such subtle shell distinction marks true biological species: hybrids of *A. proxima* and *A. lenticula* suffer gametic disgenesis producing effective sterility. Thus, in the eastern triodopsines, Grimm's (1975) and Hubricht's (1953, 1985) assertions that *messana* and *hopetonensis,* as well as *obsoleta* and *hopetonensis,* live in sympatry without conchological evidence of hybridizing cannot necessarily be rejected (as Vagvolgyi, 1968, did) simply because of the subtlety of their shell differences, because apparent integrades exist elsewhere, or because—as reported in this paper—their genitalia appear identical.

In view of these considerations, there simply is not enough evidence on which to base a robust species-level revision of eastern triodopsines at the present time. Therefore Hubricht's (1985) species designations have been retained in the supraspecific revision (Appendix C).

Recommendations for future research

The nature and definition of a species need to be researched for eastern triodopsines. Because this is now one of the phylogeneti-

cally best understood groups of pulmonates, such investigations will yield important generalizations concerning pulmonate systematics.

In addition, despite the general congruence between the two data sets (genitalic and allozymic) used for phylogenetic reconstruction, there are several problematic groups for which data were incomplete or in conflict. (1) The taxonomic status of *Webbhelix multilineata chadwicki* needs to be assessed (see Webb, 1952). (2) The zone of potential contact or integradation between *Neohelix albolabris albolabris* and *N. major* needs collection and assessment. (3) The precise ranges of *N. albolabris hubrichti* and *N. alleni alleni,* and the degree of range overlap and sympatry, need to be determined. (4) Topotypic *"Neohelix albolabris traversensis"* needs collection and dissection to test the prediction that it is *N. albolabris albolabris* which conchologically converges on *solemi;* if it is anatomically what has been called *solemi,* then the name *traversensis* has precedence for this species. (5) The status of *Neohelix lioderma* is in question: is it merely a small-sized population of *N. divesta?* (6) The systematic and ecological relationships of *Xolotrema fosteri* and *X. occidentalis* need evaluation; for example, do other *"occidentalis's"* (flat-spired cliff dwellers) occur as ecophenotypic variants within the range of *fosteri?* (7) One of the most promising areas of investigation is in the *Xolotrema denotata* group. Despite a basic sameness of the aperture and of the penial morphology, and despite evidence of hybridization, shell variation is extreme. It ranges from subglobose, with a rounded periphery, bearing periostracal hairs, and ribless *(denotata);* to depressed, with a keeled periphery, hairless, and strongly ribbed *(obstricta).* These are the only hairy shells and the only keeled shells in the eastern American triodopsines. Vagvolgyi's (1968: Fig. 21) claim that *caroliniensis* is a hybrid zone around the circular range of *obstricta* where it is nearly surrounded by the range of *denotata* is quite plausible, but needs to be tested electrophoretically and by more rigorous shell analysis. The ecological significance, if any, of the disjunct shell forms has yet to be investigated. (8) The question of whether *Triodopsis claibornensis* is a local ecophenotypic dwarf of *T. vulgata* needs to be settled. (9) Likewise, what is the status of *Triodopsis picea* in relation to *T. fraudulenta?* Does its ecological separation (high-montane) and its shell differentiation (dwarf, pustulose) denote incipient or full speciation, or ecophenotypic variation? (10) The phylogenetic position of *Triodopsis platysayoides* as sister to the *T. vulgata* group needs corroboration from an independent data set to be considered truly robust, because of its aberrant, unique penial morphology. (11) The electrophoretic similarity of *Triodopsis burchi* to *Neohelix,* in addition to its unique dorsal-pilastral sculpture of uncertain homology, make it a problematic species. It clearly needs further comparisons. (12) The phylogenetic position of the *Triodopsis tennesseensis* group is in question, and needs testing by other data sets. The possibility needs to be investigated that *T. complanata* is an ecophenotypic variant of *T. tennesseensis,* its glossiness due to living near water. If the two are true species, do they hybridize? (13) Electrophoresis of *fulciden* should clarify its now dubious placement in the *rugosa* group. (14) The *Triodopsis cragini* group, despite its disjunctly different penial morphology, parallels the variation of the *T. fallax* subgroup. Vagvolgyi's (1968) claim of hybridization, rejected by Cheatum & Fullington (1971) and Hubricht (1985), deserves electrophoretic testing. Any shell studies should explore ecological correlations. (15) Since *Triodopsis anteridon's* range lies within that of *T. tridentata,* is it an ecological variant (confusingly convergent, by the way, on *T. rugosa*)? If not, do the two species interact? (16) The Grimm-Hubricht hypothesis on the evolution of the *fallax* subgroup (Appendix D) needs rigorous testing. Grimm's unpublished lab-hybridization data and specimens should be evaluated. Multivariate shell morphometrics, coupled with targeted mitochondrial DNA studies, should resolve the problem of this intriguing evolutionary microcosm. (17) The *Triodopsis juxtidens-T. discoidea* pair seems to be a case of incipient or recent speciation involving a major shift in habitat accompanied by an apparently adaptive shell change. Vagvolgyi (1968) claimed conchological intermediates between *juxtidens* and *discoidea* in the Kanawha River Valley of West Virginia, suggesting that speciation is not complete. Careful investigation of this system, including ecological analyses and tests for directional selection for a flattened spire may be the best approach to generalities about the speciation process in triodopsines.

The eastern triodopsines, because of their species diversity, their robust phylogenetic

hypothesis, their mapped species' ranges, and their broad conchological, genitalic, and allozymic variation, are a superlative system for further evolutionary studies. For example, the three major clades *(Neohelix, Triodopsis,* and *Xolotrema)* could be compared as to (1) their modes of speciation; (2) their covariations among the respective evolutionary rates of anatomy, shell, and allozymes; (3) their phylogenetic changes in shell ontogeny, as measured from sections or x-rays of adult shells (Raup, 1966; Schindel, in review, 1986); (4) their rates of spread from Pleistocene refugia as determined by allozymic geographic variation; (5) their strengths of selection—measured by comparing dead shells of juveniles with the juvenile whorls of living adults—in parallel adaptive trends (e.g., flattening of the spire as an adaptation for cliff dwelling); and (6) their ecophenotypic plasticity of shell shape.

Perhaps the most promising aspect of the eastern triodopsines for the study of evolution is that their conchological radiation has been reiterated by the distantly related, confamilial genus *Mesodon* (Pilsbry, 1940; Emberton, 1986). These two radiations overlap each other almost perfectly in geography, ecology, conchology, and species richness (Emberton, 1986). Thus *Mesodon* represents a natural, in situ replication of the evolution of the eastern triodopsines. Such synchronous, sympatric, parallel radiations appear to be quite rare in nature, and present untapped opportunities for formulating and testing general hypotheses concerning evolutionary convergence. Since convergence can only be evaluated in the context of phylogeny (e.g., Bookstein et al., 1986), this monograph and a parallel monograph in progress on *Mesodon* lay groundwork for utilizing this system.

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APPENDIX A. ELECTROPHORETIC PROCEDURES

Loci. The 16 loci are listed in Table 12.

Gels. 33 grams starch (Electrostarch Company, lot #392) to 250 ml buffer. Dimensions 18.4 mm × 14.4 mm × 0.6 mm.

Paper wicks. Cut from filter paper, dimensions 7–8 mm × 1.2–1.3 mm; 25–30, rarely up to 40, per gel.

Buffer systems and running times. All were run at 35 milliamperes or 350 volts, whichever was reached first. TC-6, Tris-Citrate pH6 (Shaw & Prasad, 1970): 2.5 hr. Poulik (discontinuous tris-citrate): 3.5 hr. TEB 9, tris-EDTA-borate pH 9.1 (Ayala *et al.*, 1973): 4.5 hr. TEB 9/8, TEB 9 gel run in TEB 8 (Shaw & Prasad, 1970) tray buffer.

Power supply. Heath Schlumberger Regulated High Voltage Power Supply; each gel run in a separate tray under a separate power supply.

Grinding buffer. Modified from Selander et al. (1971): 0.01 molar Tris buffer, 0.001 molar EDTA, 5×10^{-5} molar NADP, 0.2 parts per thousand beta-mercaptoethanol, pH adjusted to 6.8. For making 500 ml: 0.6055 g Tris, 0.1681 g EDTA, 19.1 ml NADP, 0.01 ml beta-mercaptoethanol. Also used de-ionized distilled water for some tissues, with no detectable difference in results.

Chemicals. All from Sigma Chemical Company.

Staining. Recipes from Shaw and Prasad (1970) unless otherwise indicated in Table 12. Stained in a tray for Got and Lap; for all others, stained using agar overlay: 10 ml of 2% agar solution (4 grams agar to 200 ml water) at 60°C per 10 ml of stain, freshly mixed at room temperature. Agar overlays conserve staining chemicals and allow the gel to be readon a light table as staining proceeds, allowing greater scoring accuracy.

Controls. Mesodon zaletus from the population at Monte Sano, Alabama (GS 20 = GS 101) was used as control on all but two runs which used the same species from White Oak Sink, Tennessee (GS 9). The runs made in 1982 had 5 controls in the center of each gel, and the runs made in 1983 had 2 controls on each end and 3 controls in the center of each gel.

Scoring. Banding patterns on gels were measured on a light table and immediately copied onto graph paper to the nearest 0.5 mm, with compensations for apparent edge effects and local distortions. Questionable bands were labeled as such on the graph paper record to aid later interpretation.

APPENDIX B. SYSTEMATIC REVIEW OF THE *NEOHELIX ALBOLABRIS* AND *ALLENI* GROUPS

The studied populations are numbered from 1 to 46 as they appear in Fig. 47.

Species group *Neohelix albolabris*
(Figs. 2d-g, 4, 29c–d, 30c–d; Tables 2, 4, 6, 7; Fig. 49)

Key characters. Penis: pilastral lappets approximately half the number of columns of wall pustules; pilaster moderately wide; wall pustules all distinct and approximately equal in size; verge large; retractor-muscle's origin distant (ca 1/2 the penial length) from the penial apex; vas deferens more than 4 times as long as the penis.

Neohelix albolabris (Say, 1816)
(Figs. 2d–g, 29c–d; Tables 2, 4, 6, 7; Fig. 49)

TABLE 12. Enzyme systems used for electrophoretic analysis.

Name	Abbreviation	Enzyme commission number	Buffer system used	Molecular structure(s)	Number of readable loci
Sorbitol dehydrogenase[1]	Sordh	1.1.1.14	TEB 9	Tetramer	1
Malate dehydrogenase[2]	Mdh	1.1.1.37	TC 6	Dimers	2
Malic enzyme[3]	Me	1.1.1.40	TEB 9	Tetramer	1
Isocitrate dehydrogenase[4]	Icd	1.1.1.42	TC 6	Dimer	1
Phosphogluconate dehydrogenase[5]	Pgd	1.1.1.44	TEB 9/8	Dimer	1
Glucose-6-phosphate dehydrogenase[6]	Gd	1.1.1.49	TEB 9/8	Dimers	2
Superoxide dismutase[7]	Sod	1.15.1.1	TEB 9/8	S-1 Dimer S-2 Tetramer	2
Glutamate-oxaloacetate transaminase[8]	Got	2.6.1.1	TEB 9	Dimers	2
Phosphoglucomutase[9]	Pgm	2.7.5.1	Poulik	Monomer	1
Leucine aminopeptidase[10]	Lap	3.4.1.1	TC 6	Monomer	1
Mannose phosphate isomerase[11]	Mpi	5.3.1.8	TEB 9	Monomer	1
Glucose phosphate isomerase[12]	Gpi	5.3.1.9	Poulik	Dimer	1
Total					16

[1]Stains slowly, streaks a bit.
[2]Clear, stains in a few minutes, keeps well.
[3]Stain: 5 ml HCl developer, 5 ml MDH substrate solution, $MgCl_2$, MTT, NADP (0.15 ml), PMS, 10 ml agar. Stains slowly, keeps well. A second locus comes up with TC 6, but is unreliable.
[4]Stains very slowly, streaks a bit. Second locus visible but too streaked to read.
[5]Must be read quickly, blurs badly if left too long.
[6]Second locus does not appear unless 5 mg NADP is added to gel before degassing, as per Brewer (1970). First locus blurs and streaks quickly, second is slow and keeps well.
[7]Comes up slowly. Better if left under fluorescent light. Disappears with time.
[8]Sometimes called asparate amino transferase. Stained in tray, recipe from Selander *et al.* (1971). Soluble (anodal) locus stains faster than mitochondria (cathodal) locus. Both streak, but in one direction, so clearly readable.
[9]Strong satellite bands which had to be learned and discounted. A second locus is clear, but with too much overlap with the first locus to be scored.
[10]Stained in tray. Stains very slowly and keeps well. A second, slow locus is too streaked to read reliably.
[11]Stain recipe from Nichols, Chapman & Ruddle (1973). Stains at a moderate rate, keeps well.
[12]Stains quickly and soon blurs with formation of satellite bands.

Comparisons

Penis. On its pilaster *albolabris* differs from *major* by the density of lappets, having more per unit length (Table 4); and by the shape of the pilastral lappets, having slightly as opposed to greatly convex surfaces (Fig. 2d, e vs. Fig. 4). The wall pustules of *albolabris* are smaller than in *major* (Table 4).

Shell. *N. albolabris* has fewer striae per unit distance than *major* (Table 7). It also differs from *major* in having a lower whorl expansion rate and a much smaller baso-columellar lip node (Table 7).

Key characters

Penis: internal length 10–16 mm; pilaster 1/20th to 1/10th as broad as the penis is long, and bearing 8–14 lappets per 2.6 mm; lappet surfaces slightly convex; wall-pustular columns 16–24 per 2.6 mm; verge 1/7th to 1/5th as long as the penis.

Shell: diameter 23–39 mm, depressed-globose, whorls 5 1/2–6; striae moderately raised, 17–26 per 2.6 mm on the 5th whorl; yellow-brown to brown; glossy to dull; whorls slowly expanding for the group; apertural lip narrow to wide for the group; basocolumellar node absent to inconspicuous; pre-apertural deflection of the body whorl moderate to weak.

Neohelix albolabris albolabris (Say, 1816) (Figs. 2d–g, 29c–d; Tables 2, 4, 6, 7; Figs. 47, 49)

Studied material

(10) OH: Athens County (Ohio 35; FMNH 214917): 12 live adults—dissected #A, B; measured shells #A, B, C. (11) PA: Chester County (GS 129; FMNH 214919): 2 live

adults, 4 tissue samples—dissected #3, 4 (measured #3); electrophoresed #1, 2, 3, 4; measured shells #3, 4. (12) WV: Preston County (GS 130; FMNH 214920); 20 live adults, 20 tissue samples—dissected #9, 11, 14 (illustrated #14); electrophoresed 8, 12, 16, 17, 20; measured shells #12, 14, 17 (illustrated #14). (13) WV: Greenbrier County (GS 139; FMNH 214921): 2 live adults—dissected #A, B; measured shells #A, B. (14) WV: Boone County (GS 142; FMNH 214922): 9 live adults—dissected #A, B, C (measured #A); measured shells #A, B, C. (15) NC: Watauga (GS 151, 152; FMNH 214924): 9 live adults—dissected #A, B, C (measured #A); measured shells #A, B, C.

Published dissections

(0) PA? (Binney, 1851, Plate VI, Fig. IV). (16) NY: Albany County (Simpson, 1901, Plate 8, Figs. 2, 3, 4, 6). (17) PA: Bucks County (Pilsbry, 1940, Fig. 488:7). (18) IN: Monroe County (Webb, 1952), Plate 4, Fig. 12:7). (19) IN: Monroe County (Webb, 1954, Plate 10, Fig. 9:16).

Key characters

Shell: striae 18–23 per 2.6 mm on the 5th whorl; color light to dark brown; surface dull; height to diameter ratio .59–.72; whorls 5.2 to 6.0; outer lip width 15–30 mm; pre-apertural body whorl deflection moderate.

Neohelix albolabris bogani Emberton, new subspecies
(Tables 2, 4, 6, 7; Figs. 47, 49)

Synonymy

Xolotrema albolabris alleni ("Wetherby" Sampson) of Webb, 1952, Gastropodia, 1 (1): 7–8, Figs. 2, 13.

Triodopsis albolabris alleni (Wetherby) of Solem, 1976, Nautilus, 90: 25–36, Figs. 1a, b, 2a, c, 8–12.

Studied material

(23) OK: Sequoyah County (FMNH 176127): 2 live adults—dissected #A, B; measured shells #A, B. (20) TX: Houston County (GS 76; FMNH 214925): 10 live adults, 10 tissue samples—dissected #1, 5, 8. (21) AR: Crawford County (GS 90; FMNH 214926): 2 live adults, 2 tissue samples—dissected #3, 4; electrophoresed #1, 2. (22) AR: Logan County (FMNH 176087): 2 live adults—dissected #A (measured #A); measured shells #A, B. (23) OK: Sequoyah County (FMNH 176144): 1 live adult—dissected; measured shell. (24) AR: Washington County (FMNH 176160): 1 live adult—dissected; measured shell. (25) AR: Washington County (FMNH 176160): 1 live adult—dissected; measured shell. (26) LA: Washington County (FMNH 195989): 1 live adult—dissected; measured shell.

Published dissections

(27) AR: Logan County (Webb, 1952, Plate 4, Fig. 13). (23) OK: Sequoyah County (Solem, 1976, Fig. 5a)—also included in studied material above.

Comparisons

Neohelix albolabris bogani has previously been confused with *Neohelix alleni alleni,* from which it differs by its penial morphology (Figs. 2d vs. Fig. 3; Table 4) and subtle aspects of shell morphology (Table 7). The two occur sympatrically at Devils Den State Park, Crawford County, AR (Fig. 46, populations 3 and 21).

This is the western subspecies of *Neohelix albolabris,* occurring west of the Mississippi from at least Texas to Arkansas, but also getting east of the River in the Delta area (Fig. 46, population 26). It differs from the eastern *N. albolabris* by several shell characters which are convergent on western *alleni:* yellower color, glossier surface, moderately higher spire, and narrower lip (Table 7). It also differs from *N. albolabris* by its denser striae, its slower whorl expansion rate, and its stronger pre-apertural deflection (Table 7). In penial morphology (Table 4) and electromorphs (Table 2, Fig. 27) it shows no significant differentiation from *albolabris albolabris.*

By shell characters, *albolabris bogani* can usually be distinguished from the sometimes sympatric *alleni alleni* by its denser striae, slower whorl expansion rate, smallness of the baso-columellar node, narrower lip, and more pronounced preapertural deflection (Table 7). At Devils Den State Park, *albolabris bogani* was smaller in diameter than *alleni;* it is not known whether they were microsympatric, as the collection covered a wide area of hardwood forest.

Key characters

Shell: striae 18–26 per 2.6 mm on the 5th whorl; color yellow-brown to light brown; surface glossy; height-to-diameter ratio .58–.68; whorls 5.2–5.7.

Remarks

Despite the virtually identical penial morphology and electromorphs, the disjunct shell morphologies and geographic ranges clearly indicate subspecific status for *bogani.* The precise range relationships still need to be worked out (to fill in the gaps in Fig. 47) before sound hypotheses can be formulated about the relative time of separation of the two subspecies of *albolabris,* but it appears likely that the Mississippi River has kept them isolated for the past 20,000–40,000 years (Delcourt & Delcourt 1981). Pilsbry (1940: 842) reported an introduction of *Neohelix albolabris* from North Carolina to Tyler, Texas, presumably in the 1890's (Fig. 47). Although it is tempting to speculate that this was the founder of *albolabris bogani,* both the degree of conchological differentiation and the widespread occurrence of this subspecies in an arid terrain argue strongly against such a theory.

The shell convergence on *alleni alleni* by which *albolabris bogani* has until now escaped detection, is intriguing. Working out the degree of range overlap and sympatry of these two trans-Mississippian species would be a worthy contribution to malacology by providing valuable data on the sympatric-convergent evolution of shell morphology and color.

This subspecies is named for Dr. Arthur Bogan of the Department of Malacology, Academy of Natural Sciences of Philadelphia.

Neohelix major (Binney, 1837)
(Figs. 4, 30c, d; Tables 2, 4, 6, 7; Figs. 47, 49)

Studied material

(28) TN: Blount County (GS-3; FMNH 214927): 7 live adults, 7 tissue samples—dissected #35; electrophoresed #1, 6, 7, 10, 22, 24, 28; measured shells #1, 3, 35. (29) TN: Meigs County (GS-105; FMNH 214928): 3 live adults, 3 tissue samples—dissected #2, 3 (measured #3); electrophoresed #1, 2, 3; measured shells #1, 2, 3. (30) SC: McCormick County (GS-176; FMNH 214930): 13 live adults, 13 tissue sample—dissected #6, 7, 8 (measured #7; illustrated #6); electrophoresed #1, 2, 3, 6, 10; measured shells #4, 6, 11 (illustrated #H). (31) SC: Aiken County (GS-179; FMNH 214933): 11 live adults—dissected #A, B, C (measured #A); examined 3 partially everted penes; measured shells #A, B, C. (32) AL: Cleburne County (GS-180; FMNH 214935): 1 live adult—examined partially everted penis; measured shell.

Comparisons

Penis. *N. major* has the largest pilastral lappets—twice as many per unit length as *albolabris* (Table 4)—with the most convex, wavy surfaces. This species also has the largest wall pustules of the *albolabris* group (Table 4). In all other aspects it is similar to *N. albolabris,* and in fact much resembles an overgrown version of this species (compare Figs. 4 and 2d).

Shell. *N. major* has the least glossy shell with the relatively narrowest lip of both the *albolabris* and *alleni* groups (Table 7). Its striae are less dense than any of these taxa except *albolabris bogani,* in which the striae are much lower and less distinct (Table 7). The shells of *N. major* and *Mesodon normalis* are often sympatric and sometimes indistinguishable (Emberton, 1986).

Key characters

Penis: internal length ca 17 mm and relatively invariable; pilaster ca 1/10th as broad as the penis is long, and bearing 4–5 lappets per 2.6 mm; lappet surfaces wavy and very convex; verge 1/8th to 1/7th as long as the penis.

Shell: diameter 27–40 mm, depressed-globose, whorls 5 1/2–6; striae moderately raised, 16–34 per 2.6 mm on the 5th whorl; brown to dark brown; dull; whorls moderately expanding for the group; apertural lip relatively narrow for the group; basocolumellar node generally conspicuous; pre-apertural deflection moderate.

Remarks

Although the differences in penial morphology between *major* and *albolabris* (Figs. 4 and 2d) are arguably slight enough to denote only subspecific distinction, the available evidence supports Hubricht's recognition of *ma-*

jor as a full (sister) species. The penial difference is extremely consistent and uniform geographically, and although *albolabris* and *major* have never been found sympatric, their differences in penial size and sculpture are comparable to those between sympatric *albolabris* and *dentifera* (Fig. 2a, d). The shell differences between *major* and *albolabris* are distinct (Table 7) and disjunct, with no sign of clinal or hybridal intergradation. The electrophoretic difference is small (Table 2) but on the order of that found among other species pairs of the *albolabris* and *alleni* groups (Fig. 26, 27). There is a need for more fieldwork in Virginia to test for range overlap or intergradation.

Species Group *Neohelix alleni*
(Figs. 7, 6b, 30a–b, 32c–d; Tables 2, 4, 6, 7; Figs. 47, 49)

Key Characters

Penis: pilastral lappets approximately equal to the number of columns of wall pustules; pilaster moderately wide to narrow; wall columns with distinct pustules or locally smooth; wall pustules equal in size, or large except baso-laterally; verge moderate to minute, apical or dorsally subterminal; retractor-muscle origin close (less than 1/3rd the penial length) to the penial apex; vas deferens less than 2 1/2 times as long as the penis.

Neohelix alleni (Sampson, 1883)
(Figs. 3, 30a–b; Tables 2, 4, 6, 7; Figs. 47, 49)

Comparisons

Penis. *N. alleni* differs markedly from the *albolabris* group *(albolabris* and *major)* by its much shorter vas deferens, its retractor muscle attachment very close to the penial apex, its relatively short verge, and its flat- and smooth-surfaced, tightly appressed, densely packed pilastral lappets (Table 4, Fig. 3). Its differences from *N. solemi* are discussed under that species.

Shell. The only single character which distinguishes the shell of *alleni* from other species of the *albolabris* and *alleni* groups is its relatively faster whorl expansion rate (Table 7). It can also be separated from *albolabris* and *solemi* by its pronounced baso-columellar node (Fig. 30a), and from *major* by its glossier surface, yellower color, and denser striae (Table 7).

Key Characters

Penis: internal length 10–18 mm; pilaster ca 1/10th as broad as the penis is long, and bearing 15–18 lappets per 2.6 mm; lappet surfaces flat and smooth, lappets closely appressed; verge apical, ca 1/10th as long as the penis.

Shell: diameter 23–38 mm, depressed to depressed-globose, whorls 5–6; striae relatively low, 16–26 per 2.6 mm on the 5th whorl; yellow to yellow-brown; glossy; whorls rapidly expanding for the group; baso-columellar node large and conspicuous; preapertural deflection slight to very slight.

Neohelix alleni alleni (Sampson, 1883)
(Fig. 3a; Tables 2, 7; Figs. 47, 49)

Studied material

(1) IA: Lynn County (GS-17; FMNH 214908): 1 live adult, 1 tissue sample—dissected; electrophoresed. (2) IA: Jackson County (GS-18; FMNH 214909): 1 live adult, 1 tissue sample—dissected; electrophoresed. (3) AR: Crawford County (GS-90; FMNH 214910): 8 live adults, 8 tissue samples—dissected #4, 5, 6; electrophoresed #1, 3, 4, 5, 8; measured shells #1, 2, 8. (4) AR: Izard County (GS-97; FMNH 214911): 15 live adults, 15 tissue samples—dissected #11, 12, 13 (measured #13; illustrated #12); electrophoresed #1, 2, 4, 5, 6, 8. (5) AR: Izard County (GS-98; FMNH 214913): 4 live adults—illustrated shells #A, B (illustrated #B). (6) IA: Clayton County (FMNH 171135): 1 live adult—dissected (measured); illustrated shell. (7) AR: Izard County (FMNH 176221): 1 live adult—dissected; illustrated shell.

Comparison

This is the western (trans-Mississippian), typical, widespread subspecies of *alleni*. It differs from its eastern counterpart in its higher-spired, yellower, glossier, more densely striate, and generally smaller shell, with a slower whorl expansion rate, a less pronounced baso-columellar node, and a more pronounced pre-apertural deflection (Table 7).

Key characters

Shell: diameter 24–30 mm, depressed-globose, whorls 5–6; striae low, 16–22 per 2.6 mm on the 5th whorl; yellow to yellow-brown: glossy; whorl expansion rate low for the species; apertural lip wide for the species; basocolumellar node small for the species; preapertural deflection pronounced for the species.

Neohelix alleni fuscolabris (Pilsbry, 1903) (Fig. 3c; Tables 2, 7; Figs. 47, 49)

Studied material

(8) AL: Madison County (GS-20; FMNH 214): 14 live adults, 17 tissue samples—dissected #7, 11, 15; electrophoresed #1, 2, 4, 5, 7, 8, 9, 10, 11, 12, 13; illustrated shells #7, 11. (9) AL: Madison County (GS-101; FMNH 214): 4 live adults, 4 tissue samples—dissected #1, 2 (measured #2; illustrated #1); illustrated shell #1.

Comparison

This is the disjunct eastern subspecies of *alleni.* For shell differences, see comparative remarks under subspecies *alleni alleni* above.

Key characters

Shell: diameter 33–39 mm, depressed, whorls 5 1/2–6; striae moderately raised, 17–20 per 2.6 mm on the 5th whorl; brownish yellow; dull for the species; whorls rapidly expanding for the species; apertual lip relatively narrow for the species; basocolumellar large and pronounced for the species; preapertural deflection very slight for the species.

Neohelix solemi Emberton, new species (Figs. 6b, 32c–d; Tables 2, 4, 6, 7; Figs. 47, 49)

Synonymy

Helix albolabris var. *maritima* Pilsbry, 1890, Proc. Acad. Nat. Sci. Phila., p. 283, 3 figs. (shell, genitalia, radular teeth). Pilsbry, 1892, Nautilus 5: 142. Walker, 1906, Ill. Cat. Moll. Michigan, part I, p. 465, fig. 13. Cockerell, 1918, Nautilus 31: 108 (Ram Island, MA). Not *Helix maritima* Draparnaud, 1805.

Triodopsis albolabris form *traversensis* (Leach) Pilsbry, 1940, Land Moll. North Amer., pp. 836–839, Fig. 489 #9 (shell). Hackney, 1944, Nautilus, 58: 56 (Beaufort, NC). Jacobson, 1945, Nautilus, 59: 68 (Westchester County, NY). Alexander, 1947, Nautilus, 60: 97 (Cape May Point, NJ).

Triodopsis albolabris (Say) of Rehder, 1949, Nautilus, 62: 121 (Lake Waccamaw, Columbus County, NC); and, in part, of McCracken & Brussard, 1980, Evolution, 34: 92 ("Moriello Orchard", NY, and "Appledore Island", ME, populations).

Triodopsis albolabris albolabris (Say) plus *T. a. major* (Binney), in part, of Vagvolgyi, 1968, Bull. Mus. Comp. Zool., 136: 145 (northeastern Coastal Plain).

Triodopsis albolabris (Say) plus *T. major* (Binney), in part, of Hubricht (1985) (northeastern Coastal Plain).

Studied material (holotype and paratypes)

(33) NC: Catawba County (GS-32; FMNH 214936): 1 live adult—dissected (illustrated); illustrated shell (illustrated). (34) NC: Columbus County (GS-39; FMNH 214937): 1 live adult—dissected; illustrated shell. (35) SC: Williamsburg County (GS-41; FMNH 214939): 1 live adult—dissected (measured); illustrated shell. (36) NC: Columbus County (GS-164; FMNH 214941): 3 live adults—dissected #A, B, C (measured #B); illustrated shells #A, B, C. (37) NC: Columbus County (GS-165; FMNH 214942): 1 live adult—dissected. (38) NJ: Cape May County (GS-208; FMNH 214943): 1 live adult, 3 tissue samples—dissected #1, electrophoresed #1, 2, 3. (39) NC: Scotland County (SC-101; FMNH 214945) (HOLOTYPES): 3 live adults, 7 tissue samples—dissected #5, 6, 7. (40) NC: Scotland County (SC-103; FMNH 214946): 3 live adults, 3 tissue samples—dissected #1, 2, 3. (41) NC: Wake County (SC-138; FMNH 214947): 1 live adult, 1 tissue sample—dissected. (42) NC: New Hanover County (SC-277; FMNH 214948): 5 live adults—dissected #A, B, C, D, E. (43) NJ: Cape May County (ANSP 63869-A2432): 6 live adults—dissected #A. (44) NJ: Cape May County (ANSP 72764-A2431): 13 live adults—dissected #A, B. (46) NY: Westchester County (ANSP 181296-A2410): 1 live adult—dissected.

Comparisons

Penis. This species is unique within *Neohelix* in having a (dorsally) subterminal pore, a

ventral pilaster, a greatly reduced dorsal pilaster, and a greatly elongated basal penis (Fig. 6b).

Shell. The only shell character distinguishing *N. solemi* from other members of the *albolabris* and *alleni* groups is its relatively dark brown color (Table 7), but there is overlap in color (Table 6), so this is not reliable for identification. Practically speaking, *solemi* need only be distinguished from *N. albolabris* and *major,* both of whose ranges appear to be parapatric to it (Fig. 47). It usually differs from *N. albolabris* by its narrower apertural lip, slightly higher spire, and slightly slower whorl expansion rate; it differs from *major* by the weakness of its baso-columellar node and by its slightly higher spire, slower whorl expansion rate, glossier surface, and slightly denser striae (Table 7). These differences are based on statistical comparisons of small samples however, and should be used only as guidelines, not as absolutes, for identification. The only reliable way to distinguish *solemi* from *albolabris* or *major* is by dissection, as shown by two misclassified shells in the discriminant analysis, discussed above.

Key characters

Penis: internal length 12–17 mm; pilaster 1/50th to 1/25th as broad as the penis is long, and bearing 14–15 lappets per 2.6 mm; pilaster abbreviated in length by the subterminal pore position; pore dorsally subterminal, mounted on a thick, fleshy pedestal; verge 1/100th to 1/20th as long as the penis; basal penis long, with 1/2 or more of the total penis length lying between the vaginal opening and the base of the sheath.

Shell: diameter 24–35 mm, depressed-globose, whorls 5–6; striae moderately raised, 16–21 per 2.6 mm on the 5th whorl; dark brown; moderately dull; whorl expansion rate relatively slow; relative apertural lip width relatively low; pre-apertural deflection moderate.

Remarks

Pilsbry (1940: 839) noticed one of the anatomical distinctions of this species—its short vas deferens—but was led by shell similarities to synonomyze it with *N. albolabris traversensis* (Leach) of Traverse City, Michigan, and nearby localities. Except for this Michigan disjunct, he reported its range (based on shell material) as Coastal Plain Maine to North Carolina; this conforms well with distributional findings based on anatomical studies (Fig. 47), which further extend the range into Coastal Plain South Carolina. No material north of Westchester County, New York has yet been anatomically verified, to my knowledge, but electrophoretic and conchological comparisons have convinced me (Emberton, McCracken, & Wooden, in preparation) that *solemi* occurs in Ulster County, New York (FMNH 214952) and York County, Maine (FMNH 214950). Although I have not yet dissected topotypic *N. albolabris traversensis* (Leach), I have little doubt about its being a different species because of its extreme western disjunction from the known range of *solemi* (Fig. 47). The discriminant analysis, as discussed above, has shown that the *albolabris albolabris* shell can be mistaken for that of *solemi.*

This species is named for Dr. Alan Solem, Curator and Head, Division of Invertebrates, Field Museum of Natural History, Chicago, eminent terrestrial malacologist and mentor.

APPENDIX C. SYSTEMATIC REVIEW OF THE SUPRASPECIFIC TAXA OF THE EASTERN AMERICAN TRIODOPSINAE

The eastern American triodopsines differ from all other polygyrids in having a single dorsal pilaster in the upper penis. As in the polygyrid genera *Vespericola, Cryptomastix,* and *Allogona,* they have a penial sheath, a retentor muscle, an upper penis, and the penial retractor muscle attaches to the vas deferens (Fig. 11), but they differ from these other genera in the following ways. First, eastern triodopsines lack both epiphallus and flagellum, both of which are present, although not always conspicuous, in *Vespericola, Cryptomastix,* and *Allogona.* Second, the basal penis of eastern triodopsines is never wider than, nor longer than, the upper penis and never contains any lobes, flaps, or nonrandom folds; this differentiates them from both *Cryptomastix* and *Allogona.* Third, when eastern triodopsines have a verge, it is always flat with a subterminal pore and terminal papillae; the verge of *Vespericola* differs in being roundly conical with a simple terminal pore. Fourth, when the shells of eastern triodopsines are large and toothless, they are also always imperforate, and therefore are readily distinguishable from the widely umbilicate large shells of *Allogona* (Fig. 46).

Therefore, any snail which (a) is east of the 100th meridian, (b) has a polygyrid shell which is not *Allogona profunda* (see Fig. 46), and (c) has a penial sheath (and retentor muscle)——is a triodopsine. The penial characters are essential for identification because on shell characters alone many eastern triodopsines are easily confused or even indistinguishable from the geographically overlapping polygyrine genus *Mesodon* (see Pilsbry, 1940; Solem, 1976; Emberton, 1986). Anatomically these two lineages are readily distinguishable by the external aspect of the uneverted penis: *Mesodon* lacks the penial sheath, the retentor muscle, and the thickened spermathecal duct of triodopsines, and its penial retractor muscle inserts on the apex of the penis rather than on the vas deferens. In addition, the thick spermathecal duct of triodopsines distinguishes them from *Mesodon*. (An easy, though destructive way to identify an adult polygyrid as a *Mesodon* or an eastern-triodopsine in the field is to lightly step on it: the penis can then be diagnosed.)

Genus *Webbhelix* Emberton, new genus
(Figs. 6a, 32a–b; Table 2; Fig. 49)

Comparisons

Webbhelix is unique among triodopsines in having the dorsal pilaster covered with uniform pustules equal in size to the wall pustules (Fig. 6a). It is also the only triodopsine known to have spiral color bands on the shell (Fig. 32b), although these are not always present.

Key characters

Penis: pilaster approximately 3/4-length, abruptly truncated basally, and covered with uniform sharply-pointed pustules equal in size to wall pustules; wall pustules arranged in approximately 25 contiguous longitudinal columns and partially fused along their columns basally; verge large, with two broad and prominent terminal papillae, and smooth-surfaced.

Shell: diameter 14.5–32 mm, depressed-globose, whorls 5 1/2–6; imperforate; thin, thin-lipped; usually marked with reddish-brown color bands.

Discussion

This genus, which occupies a basal phylogenetic position, is named for Dr. Glenn R. Webb, recently retired from Kutztown University, Pennsylvania, whose forty years of dedicated research and publishing are so basic to our understanding not only of eastern triodopsines but of many other North American land pulmonates.

Webbhelix multilineata (Say, 1821)
(Figs. 6a; 32a–b; 32a–b; Table 2; Fig. 49)

Studied material

(1) IL: Marshall County (GS 127; FMNH 214848): 2 live adults, 2 tissue samples—dissected #2 (illustrated #2); electrophoresed #1; illustrated shell #2. (2) IL: Kane-Cook Counties: (GS 207; FMNH 214849): ca 11 live adults, 15 tissue samples—dissected #1, 5, A; electrophoresed #1, 3, 5. (3) IL: Calhoun County: (Hubricht 48600) ca 15 live adults—dissected #A, B, C.

Published anatomies

(1) Binney 1851, Plate VIII. (2) Webb 1948, Figs. 2, 2a. (3) Webb 1952, Plate 5, Figs. 1–8. (4) Webb 1954, Plate 10, Fig. 10.

Discussion

Webb (1952: 8) elevated Pilsbry's (1940: 850) form *chadwicki* (Ferriss, 1907) to a full species, but both Vagvolgyi (1968) and Hubricht (1985) synonymized it with *multilineata*.

Genus *Neohelix* von Ihering, 1892
(Figs. 2–5, 6b, 29–31, 32c–d; Table 2; Fig. 49)

Comparisons

Neohelix is the only genus of eastern triodosines which has pilastral lappets (Figs. 2b, e; 5c, f). It is the only genus besides *Webbhelix* which has its wall pustules arranged in 25–35 contiguous, longitudinal columns; which has a large verge, although its verge size varies; and which has a large, toothless, imperforate shell. Its shell and apertural lip seem to be always thicker than in *Webbhelix* and its shell is never banded as in *Webbhelix*. *Neohelix* also differs from

Xolotrema and *Triodopsis* in never having a ventrally subterminal pore and in never having either a palatal or a basal apertural barrier. It differs from *Triodopsis* in having a closed umbilicus. Generally, any eastern triodopsine with a shell which is imperforate, smooth-lipped, and unbanded is a *Neohelix*.

Key characters

Penis: dorsal pilaster full-length, smoothly terminating basally, and armed with lappets, lappet number either approximately the same or approximately twice the number of columns of wall pustules, pilaster rarely vestigial; wall pustules arranged in 25–35 contiguous, longitudinal columns, and either uniform in size or larger basally; verge large to vestigial, always with a corded surface and thin terminal papillae; pore terminal or, rarely, dorsally subterminal.

Species Group *Neohelix albolabris*

See Appendix B.

Species group *Neohelix alleni*

See Appendix B.

Species group *Neohelix dentifera*
(Figs. 2a–c, 5, 29a–b, 31; Table 2; Fig. 49)

Comparisons

Penis. The *dentifera* group differs from other *Neohelix* in the doubled number of its pilastral lappets (Figs. 2a, 5a, d) and the incomplete lateral fusion of the lappets' component pustules (Figs. 2b, 5c, f), as well as in the enlargement of its basal-most wall pustules (Figs. 2a, 5a, d).

Shell. The *dentifera* group's shell is much more depressed than in other *Neohelix* (Figs. 29b, 31b, d). The only species of this group which occurs east of the Mississippi, *dentifera,* is readily distinguished from all other eastern *Neohelix* by its well developed parietal tooth and wide apertural lip (Fig. 31a); the parietal tooth which occurs rarely in *albolabris* (e.g. Pilsbry, 1940, fig. 489 #8) is always much weaker than *dentifera's*.

Key characters

Penis: pilastral lappets equal in number to approximately twice the number of columns of body wall pustules; pilastral pustules comprising the lappets only partially fused laterally; basal-most wall pustules large; verge large, terminal.

Shell: diameter 16–30 mm, depressed, whorls 4 1/2–5 1/2; parietal tooth absent or strong; lip smooth or with a small bump suggesting a basal tooth or lamella (Fig. 29a); lip narrow to broad; striae weak to moderately strong.

Species subgroup *Neohelix dentifera*
(Figs. 2a–c, 29a–b; Table 2; Fig. 49)

Key characters

Penis: basal-most 2–3 layers of wall pustules enlarged.

Shell: diameter 20–30 mm, whorls 5–5 1/2; parietal tooth strongly developed; apertural lip very thick and wide; basal lip sometimes with a bump suggesting a tooth or lamella; striae moderately strong.

Neohelix dentifera (Binney, 1837)
(Figs. 2a–c, 29a–b; Table 2; Fig. 49)

Studied material

(1) WV: Preston County (GS-130; FMNH 214809): 20 live adults, 20 tissue samples—dissected #2, 7, 14; electrophoresed #1, 2, 5, 15, 16. (2) WV: Pendleton County (GS-134; FMNH 214810): 10 live adults, 10 tissue samples—dissected #1, 4, 8 (illustrated #8); electrophoresed #5; illustrated shell #8.

Species subgroup *Neohelix divesta*
(Figs. 5d, 21; Table 2; Fig. 49)

Key characters

Penis: Basal-most 8–15 layers of wall pustules enlarged.

Shell: Diameter 14–18 mm; whorls 4 1/2–5; parietal tooth always absent; apertural lip evenly narrow and always perfectly smooth internally; striae weak.

Neohelix divesta (Gould, 1848)
(Figs. 5d–f, 31c–d; Table 2; Fig. 49)

Studied material

(1) AR: Crawford County (GS-90; FMNH 214813): 1 live adult, 2 tissue samples—dissected #1, 7, 8, 10 (illustrated #1);

electrophoresed #1, 2; illustrated shell #A (FMNH 214815). (2) AR: Logan county (GS-95; FMNH 214814): ca 4 live adults, 19 tissue samples—electrophoresed #3, 9, 13, 16, 18.

Neohelix lioderma (Pilsbry, 1902)
(Figs. 5a–b, 31a–b; Table 2; Fig. 49)

Studied material

(1) OK: Tulsa County (GS-82; FMNH 214844): 9 live adults, 15 tissue sample—dissected #9, A, B, C (illustrated #A); electrophoresed #1, 5, 6, 7, 9, 10, 12, 13, 14, 15; illustrated shell #A.

Remarks

N. lioderma was originally described as subspecies of the polygyrine *Mesodon indianorum* (see Pilsbry, 1940). It is obviously a very recently derived diminutive of *divesta*, with a restricted, relict range peripheral to that of *divesta* (Fig. 49).

Genus *Xolotrema* (Rafinesque, 1819)
(Figs. 7, 8, 33, 34; Table 2; Fig. 49)

Comparisons

Penis. *Xolotrema* differs from the other three genera of eastern triodopsines by the gradual dorsal enlargement of its pustules (wall-to-pilaster); its Type 3 chevron; and its very small, apical or ventrally subterminal—never dorsally subterminal—verge.

Shell. Conchologically, *Xolotrema* is unique among eastern triodopsines in its long, smoothly curved parietal tooth which never abruptly changes height; its long, blade-like basal lamella; and its basally-pointing palatal tooth (Figs. 33a, c, e; 34a, c). It includes the only triodopsines with an angular (Figs. 33d, 34b, d) or keeled (Fig. 33f) periphery, or with hair-like periostracal processes (Fig. 33a, b). *Xolotrema* can always be distinguished from *Webbhelix* and *Neohelix* by its possession of a palatal tooth and a basal lamella, and from *Triodopsis* by the complete coverage of its umbilicus by an extension of the reflected apertural lip in the adult.

Key characters

Penis: pustules gradually enlarging dorsally, largest on the pilaster; pilastral pustules arranged either in a single column of abutting cubes or in 5 broad, nested A-shapes; wall pustules arranged in tapered, slightly separated columns all merging ventrally into 6–10 U-shapes; verge small, bearing 4–6 narrow terminal papillae; verge either terminal or ventrally subterminal and apically directed; everted penis either tubular or shaped like an everted pear; ventral sperm groove present or absent; sheath either covering entire upper (uneverted) penis or covering less than half.

Shell: diameter 8–27 mm, depressed, whorls 4 1/2–5 1/2; periphery keeled, angular, or rounded; parietal tooth long, high-standing, gently arched, smoothly decreasing in height toward the umbilicus; basal barrier in the form of a long, blade-like lamella; palatal tooth very strong to weak, pointing downward toward the basal lamella; striae either very to moderately strong, or weak and masked by dense hair-like periostracal processes.

Species group *Xolotrema fosteri*
(Figs. 8, 34; Table 2; Fig. 49)

Key characters

Penis: pilastral pustules a single column of abutting cubes; verge terminal, bearing 6 terminal papillae; everted penis tubular; ventral sperm groove present; sheath entirely covering uneverted upper penis.

Shell: diameter 14–20, whorls 4 1/2–5 1/2; periphery slightly angled or with an angled shoulder; palatal tooth moderate to weak; striae moderately strong to strong; surface free of pustules or hair-like processes.

Xolotrema fosteri (F. C. Baker, 1932)
(Figs. 8a, 34a–b; Table 2; Fig. 49)

Studied material

(1) KY: Hancock County (H-22; FMNH 214817): 1 live adult—dissected #A, B, C, D, E (illustrated #A); illustrated shell #15. (2) KY: Hancock County (GS-15; FMNH 214819): 24 live adults, 24 tissue samples—dissected #19; electrophoresed #12, 13, 14, 15, 16, 17, 18, 19, 21, 22.

Xolotrema occidentalis (Pilsbry & Ferriss, 1907)
(Figs. 8b–c, 34c–d; Table 2; Fig. 49)

Studied material

(1) AR: Independence County (GS-99; FMNH 214855): 1 live adult, 10 tissue samples—electrophoresed #2, 3. (2) AR: Independence County (GS-100; FMNH 214856): 5 live adults, 10 tissue samples—dissected #5 (illustrated #5); electrophoresed #1, 2, 3, 4, 10; illustrated shell #5.

Species group *Xolotrema denotata*
(Figs. 7, 33; Table 2; Fig. 49)

Key characters

Penis: pilastral pustules in 5 broad, nested A-shapes; verge subterminal, apically directed, bearing 4 terminal papillae; everted penis shaped like an inverted pear; ventral sperm groove absent; sheath covering less than half the uneverted upper penis.

Shell: diameter 17–26 mm, whorls 5–6; periphery keeled, to angled, to rounded; palatal tooth very strong; striae either very to moderately strong, or weak and masked by sense hair-like periostracal processes.

Xolotrema denotata (Férussac, 1821)
(Figs. 7a–b, 33a–b; Table 2; Fig. 49)

Studied material

(1) IN: Jefferson County (GS-14; FMNH 214805): 0 live adults, 2 tissue samples—electrophoresed #1, 2. (2) KY: Fayette County (GS-112; FMNH 214806): 7 live adults, 13 tissue samples—dissected #1, 2, 6 (illustrated #6); electrophoresed #1, 2, 5, 6, 7, 8, 10, 11, 13; illustrated shell #1.

Xolotrema obstricta (Say, 1821)
(Figs. 7c–d, 33e–f; Table 2; Fig. 49)

Studied material

(1) KY: Henderson County (GS-16; FMNH 214852): 1 live adult, 1 tissue sample—electrophoresed #1; illustrated shell #1. (2) AL: Madison County (GS-20; FMNH 214853): 1 live adult, 1 tissue sample—electrophoresed #1. (3) KY: Edmonson County (GS-125; FMNH 214854): 15 live adults, 16 tissue samples—dissected #1, 9 (illustrated #9); electrophoresed #1, 3, 4, 6, 10.

Xolotrema caroliniensis (Lea, 1834)
(Figs. 7e, 33c–d; Table 2; Fig. 49)

Studied material

(1) AL: DeKalb-Marshall Counties (GS-184; FMNH 214): 1 subadult, 1 tissue sample—electrophoresed #1. (2) TN: Franklin County (FMNH 171142): 5 live adults—dissected #A, B (illustrated #A); illustrated shell #B.

Genus *Triodopsis* (Rafinesque, 1819)
(Figs. 9–18, 35–45; Table 2; Fig. 49)

Comparisons

Penis. *Triodopsis* differs from the other three genera of eastern triodopsines by the abruptly larger pustules on its pilaster.

Shell. *Triodopsis* is unique among eastern American triodopsines in having an open umbilicus and a distinct, non-lamellar basal tooth.

Key characters

Penis: pilastral pustules abruptly larger than wall pustules; pilastral pustules either unfused, fused into nesting horeshoe shapes, fused into two columns of interdigitating rectangular box shapes, fused into grossly irregular elements, fused into a solid apical mass bearing three to four tiers of long and sharp spurs, or fused into irregular polygons bearing short and blunt spurs; wall-pustular columns separated and either radiating from the pore, 15–20 (or rarely 8–10) in number, and unmerging or incompletely merging basally; or completely merging ventrally to form either 10–12 obtuse V-shapes or 5–7 acute V-shapes; wall-pustular columns with pustules distinct, with pustules partially fused, or smooth with no sign of pustules; verge absent; pore terminal or ventrally subterminal; penis short, to long, to extremely long and thread-like; erectile, fleshy peduncle below the pore large, small, or absent.

Shell: diameter 8–27 mm, depressed-globose to depressed, whorls 4 1/2–6 1/2; umbilicus wide and open to minute and creviced; parietal tooth prominent, varying from straight to abruptly angled up to about 120 degrees, from uniformly high-standing to abruptly changing in height; basal tooth weak (rarely absent) to pronounced, varying from peg-like to tapered, from simple to buttressed to bidentate, and from marginal to deeply re-

cessed; palatal tooth pointing toward the umbilicus, weak (rarely absent) to pronounced, varying from broad to narrow, from squared to tapered, from simple to buttressed, and from marginal to deeply recessed; striae very weak to very strong.

Species group *Triodopsis vulgata*
(Figs. 9, 10, 35, 36; Table 2; Fig. 49)

Key characters

Penis: pilastral pustules unfused or fused into nesting horseshoe shapes; wall pustular columns 15–20, radiating from the pore, unmerging or partially merging basally, and either with distinct pustules or nearly smooth; pore ventrally subterminal, about 1/5-way from the apex, everted penis shaped like an angled baseball bat.

Shell: diameter 10–19.5 mm, depressed, whorls 4 1/2–6; aperture deeply dished; apertural periphery with a squared-off appearance; parietal tooth straight, broadly wedge-like, and symmetrical or slightly angled and tapered toward the umbilicus; basal tooth peg-like, marginal; palatal tooth broad, squared, recessed; striae moderate to very strong.

Species subgroup *Triodopsis vulgata*
(Figs. 9a, c; 35a, b, e, f; Table 2; Fig. 49)

Key characters

Penis: pilastral pustules unfused; wall pustular columns never merging.

Shell: parietal tooth slightly angled and tapered toward the umbilicus.

Triodopsis vulgata Pilsbry, 1940
(Figs. 9a, 35a–b; Table 2; Fig. 49)

Studied material

(1) TN: Morgan County (GS-109; FMNH 214883): 20 live adults, 18 tissue samples—dissected #2, 3. (2) KY: Fayette County (GS-112; FMNH 214884): 7 live adults, 8 tissue samples—dissected #1 (illustrated #1); electrophoresed #1, 2, 3, 4, 6, 7, 8; illustrated shell #A. (3) KY: Harlan County (GS-119; FMNH 214885): 9 live adults, 11 tissue samples—dissected #1, 2, 3, 4; electrophoresed #2, 3, 6.

Triodopsis claibornensis Lutz, 1950
(Figs. 9c, 35e–f; Table 2; Fig. 49)

Studied material

(1) TN: Claiborne County (GS-117; FMNH 214800): 22 live adults, 22 tissue samples—dissected #5, 18 (illustrated #18); electrophoresed #1, 5, 16, 20; illustrated shell #A.

Species subgroup *Triodopsis fraudulenta*
(Figs. 9b, 10, 35c–d, 36; Table 2; Fig. 49)

Key characters

Penis: pilastral pustules fused into nesting horseshoe shapes; wall-pustular columns unmerging or partially merging basally, with distinct pustules or nearly smooth.

Shell: parietal tooth straight, broadly wedge-like, and symmetric.

Triodopsis fraudulenta (Pilsbry, 1894)
(Figs. 10, 36; Table 2; Fig. 49)

Studied material

(1) WV: Greenbrier County (GS-139; FMNH 214822): ca 5 live adults, 11 tissue samples—dissected #6, 8 (illustrated #6); electrophoresed #2, 4, 5, 6, 7, 11; illustrated shell #A.

Triodopsis picea Hubricht, 1958
(FIgs. 9b, 35c–d; Table 2; Fig. 49)

Studied material

(1) WV: Pendleton County (GS-134; FMNH 214860): 20 live adults, 20 tissue samples—dissected #4, 14 (illustrated #14); electrophoresed #1, 5, 9, 11, 17; illustrated shell #15.

Species group *Triodopsis platysayoides*
(Figs. 12, 37; Table 2; Fig. 49)

Key characters

Penis: pilastral pustules fused into two columns of interdigitating rectangular box shapes; wall-pustular columns completely merging ventrally to form 10–12 obtuse V-shapes; pore terminal.

Shell: diameter 27 mm; spire nearly flat; umbilicus very broad and open; parietal tooth short, nearly straight, high-standing, symmet-

rical, and scooped internally; basal tooth very low, with broadly tapered sides; palatal tooth absent.

Triodopsis platysayoides (Brooks, 1933)
(Figs. 12, 37; Table 2; Fig. 49)

Studied material

(1) WV: Preston County (SC-273; FMNH 214861): 2 live adults, 5 tissue samples (collected under U.S. Dept. Interior Fish & Wildlife Permit # PRT-670226 and W. Va. Dept. Nat. Res. Scientific Collecting Permit No. 17, 1984, both to the author)—dissected #1, 2 (illustrated #1); electrophoresed #1, 3, 4, 5; illustrated shell #2. (2) WV: Preston County (Hubricht 11860): 1 live adult—examined dissection done by Solem (1976).

Species group *Triodopsis burchi*
(Figs. 11a, 37a–b, Table 2; Fig. 49)

Key characters

Penis: pilastral pustules fused into grossly irregular elements irregular in size and shape; wall-pustular columns ca 15, radiating from the pore, unmerging, and semi-smooth; pore terminal.

Shell: diameter 8–17 mm; spire extremely low; parietal tooth as in the *platysayoides* group; palatal tooth high, tiny, triangularly pointed, and marginal.

Triodopsis burchi Hubricht, 1950
(Figs. 11a, 37a–b; Table 2; Fig. 49)

Studied material

(1) VA: Patrick County (GS-143; FMNH 214797): ca 10 live adults, 14 tissue samples—dissected #3, 5, 12 (illustrated #3); electrophoresed #3, 4, 7, 9, 11, 14; illustrated shell #10.

Species group *Triodopsis tennesseensis*
(Figs. 11b–d, 37c–f; Table 2; Fig. 49)

Key characters

Penis: pilastral pustules fused into a solid apical mass bearing three to four tiers of long, sharp spurs; wall-pustular columns as in the *burchi* group, except completely smooth.

Shell: diameter 9–25 mm; spire low; apertural teeth as in the *burchi* group; striae either very strong or very weak.

Triodopsis tennesseensis (Walker & Pilsbry, 1902)
(Figs. 11b–c, 37c–d; Table 2; Fig. 49)

Studied material

(1) KY: Fayette County (GS-112; FMNH 214864): 18 live adults, 18 tissue samples—dissected #13, 14, 15 (illustrated #15); electrophoresed #2, 5, 18; illustrated shell #7. (2) KY: Pulaski County (GS-124; FMNH 214865): 7 live adults, 12 tissue samples—electrophoresed #1, 6.

Triodopsis complanata (Pilsbry, 1898)
(Figs. 11d, 37e–f; Table 2; Fig. 49)

Studied material

(1) KY: Pulaski County (GS-13; FMNH 214802): 0 live adults, 1 tissue samples—electrophoresed #1, 2. (2) KY: Pulaski County (Hubricht 17932): ca 9 live adults (live into isopropynol)—dissected #A, B, C (illustrated #C); illustrated shell #A.

Species group *Triodopsis rugosa*
(Figs. 18b, 45c–d; Table 2; Fig. 49)

Key characters

Penis: pilaster ca 2/3-length and proximally tapered; pilastral pustules fused to form irregular polygons each bearing 1–3 short, blunt spurs; wall-pustular columns either ca 15 or ca 9, partially fused basally, semi-smooth; pore terminal.

Shell: diameter 8–11 mm; depressed; umbilicus moderate; parietal tooth as in the *vulgata* group; basal and palatal teeth peg-like, strongly buttressed, slightly recessed; striae very strong, modertaely to widely spaced.

Triodopsis rugosa Brooks & Macmillan, 1940
(Fig. 49)

Studied material

(1) WV: Logan County (SC-278; FMNH 214888): 6 live adults, 11 tissue samples—dissected #1, 2.

Triodopsis fulciden Hubricht, 1952
(Figs. 18b, 45c–d; Table 2; Fig. 49)

Studied material

(1) NC: Burke County (GS-35; FMNH 214823): 5 live adults, 5 tissue samples—dissected #3 (illustrated #3); electrophoresed #2, 3; illustrated shell #A.

Species group *Triodopsis cragini*
(Figs. 13, 39; Table 2; Fig. 49)

Key characters

Penis: penis extremely long and thread-like; pilaster as in the *rugosa* group; wall-pustular pilaster columns completely fused ventrally into 5–7 acute V-shapes.

Shell: diameter 8.5–14.5 mm; depressed-globose; umbilicus small; parietal tooth slightly to pronouncedly scooped externally, umbilicad extension moderate to absent; basal tooth with an umbilicad extension varying from weak to equal in size to the basal tooth itself, and slightly to deeply recessed; basal lip bearing a weak to strong convex ridge; palatal tooth broad, rounded, and varying from moderately sized and recessed to very large and deeply recessed; striae weak to strong.

Remarks

The shells of the three species seem to form a continuum from least to most derived in the order *cragini, vultuosa, henriettae*, showing an increasing overgrowth of the apertural lip and dentition. This hypothesis is supported by the electrophoretically more primitive position of *cragini* in the Wagner-2 Tree (Fig. 27) and as depicted in the Consensus Tree (Fig. 28).

Triodopsis cragini Call, 1886
(Figs. 13b, 39c–d; Table 2; Fig. 49)

Studied material

(1) TX: Polk County (GS-73; FMNH 214803): 20 live dults, 20 tissue samples—dissected #3, 18 (illustrated #18); electrophoresed #1, 2, 4, 8, 10, 14; measured shell #2. (2) TX: Henderson County (GS-79; FMNH 214804): 7 live adults, 7 tissue samples—electrophoresed #2, 3, 6.

Triodopsis vultuosa (Gould, 1848)
(Figs. 13a, 39a–b; Table 2; Fig. 49)

Studied material

(1) TX: Walker County (GS-71; FMNH 214887): 18 live adults, 15 tissue samples—dissected #A, B (illustrated #A); electrophoresed #1, 9, 11; illustrated shell #7. (2) TX: Cherokee County (GS-78; FMNH uncat.): ? live adults, 11 tissue samples—electrophoresed #1, 6. (3) TX: Jefferson County (GS-208?; FMNH uncat.): ? live adults, ? tissue samples—electrophoresed #1, 2.

Triodopsis henriettae (Mazÿck, 1877)
(Figs. 13c, 39e–f; Table 2; Fig. 49)

Studied material

(1) TX: Houston County (GS-76; FMNH 214824): 2 live adults, 2 tissue samples—dissected #1, 2 (illustrated #2); electrophoresed #1, 2; illustrated shell #2.

Species group *Triodopsis tridentata*
(Figs. 14a–b, 14, 16, 17, 40, 42, 43, 44; Table 2; Fig. 49)

Key characters

Penis: penis length moderate; pilaster as in the *rugosa* and *cragini* groups; pore ventrally subterminal, ca 1/4-way from the apex; everted penis mace-shaped; moderate-sized peduncle beneath pore.

Shell: diameter 8–15 mm; depressed-globose to depressed; whorls 4 1/2–6 1/2; umbilicus moderate to minute; parietal tooth variable, ranging from that of the *vulgata* and *fraudulenta* groups, to that of the *burchi* and *tennesseensis* groups, to that of the *cragini* group with a more pronounced umiblicad extension, to a form superficially resembling that of the *denotata* group of *Xolotrema;* basal tooth marginal and variable, covering much of the range of shapes found in the *vulgata*, *rugosa*, and *cragini* groups, and rarely absent entirely; palatal tooth marginal and supraperipheral, to moderately recessed and subperipheral, and either peg-like (and buttressed or unbuttressed), or as in the *cragini* group (and buttressed or unbuttressed), or rarely absent; striae very weak to very strong.

Species subgroup *Triodopsis tridentata* (Figs. 14a–b, 40; Table 2; Fig. 49)

Key characters

Shell: diameter 12–15 mm; depressed; whorls 4 1/2–5 1/2; umbilicus moderate; parietal tooth either as in the *rugosa* group or as in the *burchi* or *tennesseensis* group; basal and parietal teeth as in the *rugosa* group, except either buttressed or unbuttressed (or rarely absent altogether), and with the palatal tooth marginal; striae very strong.

Triodopsis tridentata (Say, 1816) (Figs. 14a, 40a–b; Table 2; Fig. 49)

Studied material

(1) TN: Blount County (GS-8; FMNH 214866): 1 live adult, 1 tissue sample—electrophoresed #1. (2) TN: Blount County (GS-9; FMNH uncat.): ? live adults, 9 tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9. (3) NC: Haywood County (GS-10; FMNH 214867): ca 10 live adults, 10 tissue samples—electrophoresed #6. (4) WV: Pendleton County (GS-134; FMNH 214875): 10 live adults, 10 tissue samples—dissected #3. (5) WV: Pocahontas County (GS-135; FMNH 214876): 4 live adults, 5 tissue samples—dissected #2 (illustrated #2); electrophoresed #1 2, 3, 4; illustrated shell #4. (6) KY: Harlan County (GS-119; FMNH 214872): 1 live adult, 1 tissue sample—dissected #1. (7) KY: Edmonson County (GS-125; FMNH 214873): 2 live adults, 2 tissue samples—dissected #1, 2. (8) WV: Preston County (GS-126; FMNH 214874): 15 live adults, 15 tissue samples—dissected #15. (9) NC: Avery County (GS-153; FMNH 214878): 10 live adults, 10 tissue samples—electrophoresed #2, 5, 7. (10) OH: Athens County: Site IV-1 (FMNH 209209): 10 live adults—dissected #C, D. (11) OH: Athens County: Site III-3 (FMNH 209536); 5 live adults—dissected #C. (12) Locality unknown (FMNH 171254): ? live adults—dissected #A.

Triodopsis anteridon (Pilsbry, 1940) (Figs. 14b, 40c–d; Table 2; Fig. 49)

Studied material

(1) KY: Harlan County (GS-121; FMNH 214793): 21 live adults, 21 tissue samples—dissected #13, 14; electrophoresed #6, 7, 16. (2) WV: Boone County (GS-142; FMNH 214796): 20 live adults, 20 tissue samples—dissected #18 (illustrated #18); electrophoresed #3, 10; illustrated shell #19.

Species group *Triodopsis fallax* (Figs. 15, 16, 17, 42, 43, 44; Table 2; Fig. 49)

Key characters

Shell: diameter 8–14 mm; depressed-globose; whorls 4 1/2–6 1/2; umbilicus moderate to minute; parietal tooth as in the *cragini* group, but with a more pronounced, angled umbilicad extension; apertural lip teeth as in the *cragini* group, but with the basal tooth marginal more strongly buttressed, the palatal tooth only slightly recessed; striae moderate to strong.

Remarks

The phylogeny of the *fallax* group is discussed in Appendix D. For species diagnoses see Grimm (1975), except for *palustris,* for which see Hubricht (1958).

Species subgroup *Triodopsis fallax* (Figs. 15b–c, 16b, 17, 42c–f, 43c–d, 44a–d; Table 2; Fig. 49)

Key characters

Shell: whorls 4.5–5.0, lip edge generally sharp, apertural teeth relatively indistinct; luster dull to very shiny.

Triodopsis fallax (Say, 1825) (Figs. 17a, 44a–b; Fig. 49)

Studied material

(1) NC: Richmond County (Hubricht 10209): 6 live adults (dropped live into isopropynol)—dissected #A, B, C (illustrated #C); measured shell #A.

Triodopsis messana Hubricht, 1952 (Figs. 16b, 43c–d; Table 2; Fig. 49)

Studied material

(1) NC: Columbus County (GS-163; FMNH 214846): ca 5 live adults, 10 tissue samples—dissected #1, 5, 6 (illustrated #6); electrophoresed #1, 7, 8, 9; illustrated shell #A.

Triodopsis palustris Hubricht, 1958
(Figs. 15b, 42c–d; Table 2; Fig. 49)

Studied material

(1) SC: Williamsburg County (GS-41; FMNH 214857): ca 5 live adults, 15 tissue samples—dissected #4, 5, 15 (illustrated #15); electrophoresed #5, 8, 10, 11, 15; illustrated shell #1. (2) GA: Wayne County (GS-49; FMNH 214858): ca 6 live adults, 15 tissue samples—electrophoresed #4, 9.

Triodopsis obsoleta (Pilsbry, 1894)
(Figs. 15c, 42e–f; Fig. 49)

Studied material

(1) NC: Chowan County (Hubricht 10300): 7 live adults (dropped live into isopropanol)—dissected #A, B, C (illustrated #C).

Triodopsis soelneri (Henderson, 1907)
(Figs. 17b, 44c–d; Fig. 49)

Studied material

(1) NC: New Hanover County (ANSP A2318): 3 live adults—dissected #A, B, C (illustrated #B). (2) NC: Columbus County (FMNH 159040): shells only-illustrated shell #A.

Species subgroup *Triodopsis alabamensis*
(Figs. 15a, 16a, c, 42a–b, 43a–b, e–f; Table 2; Fig. 49)

Key characters

Shell: whorls 4 1/2–6 1/2; lip edge swollen; apertural teeth relatively distinct; luster always dull.

Triodopsis alabamensis (Pilsbry, 1902)
(Figs. 27a, 54a–b; Table 8; Fig. 49)

Studied material

(1) TN: Meigs County (GS-105; FMNH 214791): 3 live adults, 7 tissue samples—dissected #2, 4 (illustrated #4); electrophoresed #1, 2, 3, 4, 6, 7; illustrated shell #A.

Triodopsis vannostrandi (Bland, 1875)
(Figs. 16c, 43e–f; Table 2; Fig. 49)

Studied material

(1) SC: Aiken County (GS-179; FMNH 214880): 12 live adults, 12 tissue samples—dissected #1, 8, 12; electrophoresed #1, 2, 3, 4, 5, 6, 10; illustrated shell #11.

Triodopsis hopetonensis (Shuttleworth, 1852)
(Figs. 15a, 42a–b; Table 2; Fig. 49)

Studied material

(1) NC: Catawba County (GS-33; FMNH uncat.): ? live adults, 12 tissue samples—electrophoresed #2, 4, 6, 9. (2) NC: Columbus County (GS-38; FMNH 214827): ca 25 live adults, 25 tissue samples—dissected #15, 25, A (illustrated #A); illustrated shell #22. (3) AL: Perry County (GS-57; FMNH 214832): ca 10 live adults, 13 tissue samples—electrophoresed #8.

Species group *Triodopsis juxtidens*
(Figs. 14c–d, 18a, c, 41, 45a–b, e–f; Table 2; Fig. 49)

Key characters

Penis: penis length moderate; pilaster as in the *rugosa, cragini, tridentata,* and *fallax* groups; wall-pustular columns as in the *cragini* and *tridentata* groups; pore ventrally subterminal, ca 2/5-way from the apex; everted penis shaped as in the *tridentata* group, but with a broader apical knob; large-sized peduncle beneath pore.

Shell: diameter 10–18 mm, moderately to very depressed, whorls 4 1/2–6; umbilicus moderately to very wide; aperture dished but not as deeply as in the *vulgata* group; parietal tooth as in the *vulgata* and *rugosa* groups and the *tridentata* group; palatal tooth marginal to moderately recessed, narrow to moderately broad, squared to pointed; basal tooth marginal, as in the *tridentata* group, but rarely buttressed on the columellar side.

Species subgroup *Triodopsis juxtidens*
(Figs. 14c–d, 18a, c, 41a–d; Table 2; Fig. 49)

Key characters

Shell: palatal tooth rounded, umbilicus moderately depressed to very depressed.

Triodopsis juxtidens (Pilsbry, 1894)
(Figs. 14c, 41a–b; Table 2; Fig. 49)

Studied material

(1) NC: Catawba County (GS-33; FMNH 214838): ca 9 live adults, 12 tissue samples—dissected #1, 2, 3; electrophoresed #2, 4, 6, 9. (2) NC: Burke County (GS-34; FMNH 214839): 1 live adult, 2 tissue samples—dissected #4. (3) NC: Columbus County (GS-37; FMNH 214840): ca 30 live adults, 30 tissue samples—electrophoresed #4, 18. (4) WV: Pendleton County (GS-132; FMNH 214841): 10 live adults, 10 tissue samples—dissected #5, 10 (illustrated #5); illustrated shell #7. (5) WV: Pocahontas County (GS-135; FMNH 214842): 10 live adults, 11 tissue samples—dissected #5, 6; electrophoresed #1, 2, 3, 8, 9.

Triodopsis discoidea (Pilsbry, 1904)
(Figs. 14d, 41c–d; Fig. 49)

Studied material

(1) IL: Hardin County (SC-217; FMNH 214811): 1 live adult, 8 tissue samples—dissected #5 (illustrated #5); illustrated shell #A.

Species subgroup *Triodopsis neglecta*
(Figs. 18a, c, 45a–b, e–f; Table 2; Fig. 49)

Key Characters

Shell: palatal tooth squared; unmbilicus moderately to very wide; depressed.

Triodopsis neglecta (Pilsbry, 1899)
(Figs. 18a, 45a–b; Table 2; Fig. 49)

Studied material

(1) MO: Barry County (GS-96; FMNH 214850): ca 7 live adults, 10 tissue samples—dissected #2, 5 (illustrated #2); electrophoresed #1, 2, 4, 5, 8; illustrated shell #A.

Triodopsis pendula Hubricht, 1952
(Figs. 18c, 45e–f; Table 2; Fig. 49)

Studied material

(1) NC: Wilkes County (GS-149; FMNH 214859): ca 5 live adults, 19 tissue samples—dissected #18 (illustrated #8); electrophoresed #1, 4, 7, 18; measured shell #14.

APPENDIX D. ON THE PHYLOGENY OF THE *TRIODOPSIS FALLAX* GROUP

The *fallax* subgroup is believed to comprise 8 species (Hubricht, 1985). Hubricht (1953, 1971) discussed field evidence for hybridization or lack of it among 6 of these species. In 1975, Grimm cursorily summarized his 10 years of field and laboratory studies on hybridization or lack of it among 7 of these species, and proposed an evolutionary hypothesis based on shell lip and dentition, presence or absence of field hybridization, and current geographical distributions. In Fig. 51, Grimm's (1975) verbal hypothesis is summarized in the form of a cladogram. Table 13 summarizes Grimm's hybridizational evidence in support of this cladogram, and adds the available genetic-distance data. One species is included *(palustris)* which Grimm omitted from his hypothesis.

It is beyond the scope of this paper to evaluate Grimm's (1975) conclusions concerning field hybridization. Grimm's specimens and notebooks are at the National Museum of Natural Sciences, Ottawa, Canada, and deserve morphometric study. The consistency of Grimm's conclusions concerning hybridization with this cladogram is apparent in Table 13: of the 10 species pairs found sympatric, those which commonly hybridize in nature have an average patristic distance (number of transformations separating them) of 2.1 ($n = 6$), those which rarely hybridize in nature have a patristic distance of 3 ($n = 1$), and those which never hybridize in nature have an average patristic distance of 4.3 ($n = 3$). It would be tautological to consider this correlation as validating Grimm's cladistic hypothesis (Fig. 51), however, because he based his hypothesis on these same hybridization data.

An independent test of the cladogram is afforded, however, by the electrophoretic data available for four of the species pairs (Table 13). The four Prevosti genetic dis-

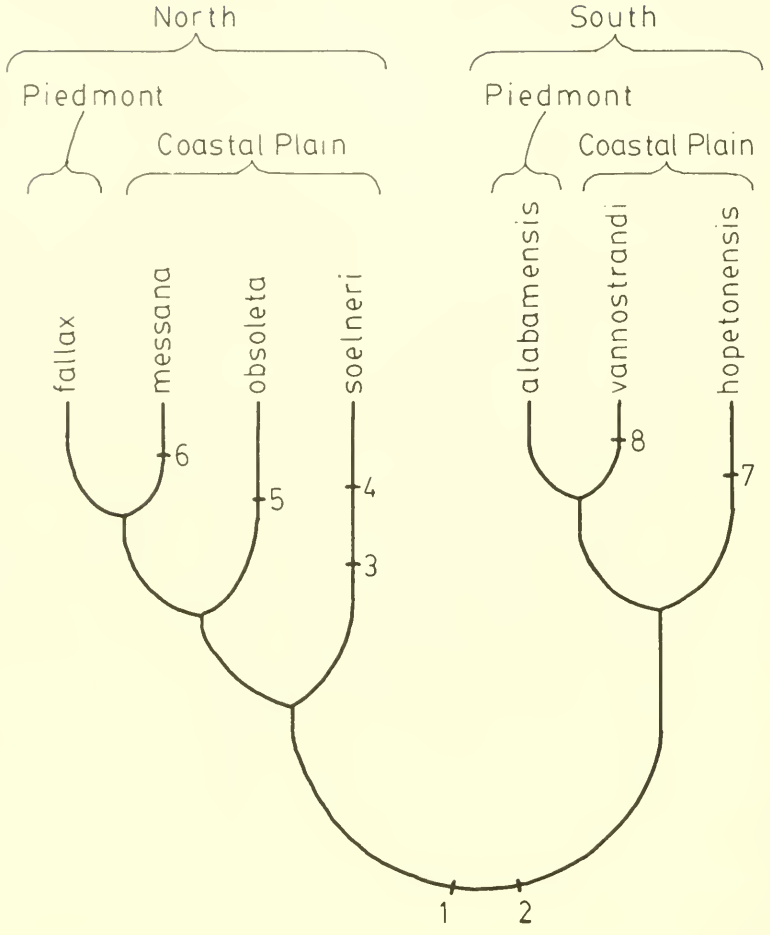

FIG. 51. Cladogram summarizing Grimm's (1975) phylogenetic hypothesis for the *Triodopsis fallax* subgroup. Hypothesized character transformations: 1. Differentiation of apertural tooth prominence into less distinct (Fig. 44a)—to the left—vs. more distinct (Fig. 43a)—to the right—with the ancestral condition unknown. 2. Differentiation of the thickness of the internal edge of the apertural lip and teeth into relatively thin—to the left—vs. relatively thick—to the right—, with the ancestral condition unknown. 3. Type A, extreme reduction of the lip teeth (from Fig. 44a to Fig. 44c). 4. Reduction of overall penial sculpture (from Fig. 17a to 17b). 5. Type B, pronounced reduction of lip teeth (from Fig. 44a to Fig. 42e). 6. Type C, moderate reduction of lip teeth (from Fig. 44a to Fig. 43c). 7. Type D, moderate reduction of lip teeth (from Fig. 43a to Fig. 42a). 8. Type E, slight reduction of lip teeth (from Fig. 43a to Fig. 43e).

tances (taken from Emberton, 1986, Appendix B-1) do not support the cladogram, as is shown below:

Cladistic distance	Genetic distance(s)
2	.32
3	.27
4	.27, .35

where "cladistic distance" equals the number of transformations separating the species in the cladogram (Fig. 51). These data are scant, and the differences not very great, so they are hardly conclusive. Because of the small and close genetic distances involved, this group has probably radiated so recently that electrophoresis will be of little value in deducing its phylogeny; of the currently available biochemical methods, mitrochondrial DNA studies are more likely to provide an-

TABLE 13. Supporting evidence for Grimm's (1975) implied cladogram of the *Triodopsis fallax* group.

Species pair	Patristic distance[a]	Genetic distance (Prevosti)	Grimm's field observations
fallax & *obsoleta*	1	—	hybrids
fallax & *alabamensis*	2	—	hybrids
fallax & *vannostrandi*	3	—	hybrids[b]
fallax & *hopetonensis*	3	—	hybrids
messana & *obsoleta*	2	—	hybrids
messana & *soelneri*	3	—	sympaters[c]
messana & *alabamensis*	3	.27	(no overlap)
messana & *vannostrandi*	4	.27	(no overlap)
messana & *hopetonensis*	4	.35	sympaters
hopetonensis & *vannostrandi*	2	.32	hybrids
hopetonensis & *obsoleta*	4	—	sympaters
hopetonensis & *soelneri*	5	—	sympaters
palustris & *messana*	?	.21	—
palustris & *alabamensis*	?	.22	—
palustris & *vannostrandi*	?	.30	—
palustris & *hopetonensis*	?	.33	—

[a]Number of transformations on Grimm's cladogram (Fig. 51).
[b]"*fallax* × *vannostrandi* × *hopetonensis*."
[c]Although a single hybrid population was found.

swers because of the faster evolutionary rate of this molecule.

According to Grimm's (1975) hypothesis, the *fallax* subgroup consists of a Piedmont stock which has successively invaded and speciated in the Coastal Plain during Plio-Pleistocene regressions, as first suggested by Hubricht (1953). The inland stock differentiated early between *fallax* in the north and *alabamensis* in the south, both with strongly developed apertural dentition. According to the hypothesis, *fallax* spun off three successive Coastal Plain species—*soelneri*, *obsoleta*, and *messana*—each with a different type of reduced dentition, and ranging from extremely reduced (Fig. 44c), to very reduced (Fig. 42e), to moderately reduced (Fig. 43c); and *alabamensis* spun off two successive Coastal Plain species—*hopetonensis* and *vannostrandi*—each with a different type of reduced dentition, and ranging from moderately reduced (Fig. 42a) to slightly reduced (Fig. 43e). Grimm suggested—for no clearly stated reason—that the longer a species of the *fallax* group remains on the Coastal Plain, the more reduced its apertural dentition becomes. Purportedly, all 7 of these species hybridize in the laboratory, but not all hybridize when they come in contact in the field (Grimm, 1975).

Based on the cladogram of Fig. 51, the *fallax* group into the two subgroups (called "herds" by Grimm, 1975) *fallax* and *alabamensis*.

T. palustris, which was not analyzed by Grimm, is tentatively placed in the (northern) *fallax* subgroup, despite its somewhat southern range (Fig. 49)—and despite Hubricht's (1950–1953) placing it with *alabamensis* for that reason—because of its less prominent teeth and relatively thin inner lip (see transformations 1 and 2, Fig. 51), and because it is electrophoretically closer to *messana* (Prevosti distance .21) than to *alabamensis*, *vannostrandi*, or *hopetonensis* (Prevosti distances .22, .30, and .33). Following Grimm's concept of evolutionary trends, *palustris's* position in the cladogram (Fig. 51) lies between *obsoleta* and *messana*, because the reduction of its lip teeth (Fig. 42c) is intermediate between those two species (Fig. 42e and 43c).

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